R. EXD.

Vol. 91. Part 8. Pp. 367–446, 81 figs. 25th November, 1941

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price £1 1s. 0d.

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THE THORAX OF THE WINGLESS AND SHORT-WINGED HYMENOPTERA

By J. A. Reid, B.Sc., A.R.C.S.

Manuscript received 20th October, 1939.

(Read 6th November, 1940.)

With Eighty-one Text Illustrations.

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I. *Introduction and Acknowledgments.*

This investigation was undertaken at the suggestion of Dr. O. W. Richards, for whose advice I am most grateful. I also offer my sincere thanks to Professor J. W. Munro, who made it possible for me to undertake the work. My thanks are also due to Mr. R. B. Benson for placing the facilities of the British Museum (Natural History) at my disposal; without access to the British Museum collection of Hymenoptera it would have been useless to have attempted the work.

It is well known that the thorax of many flightless Hymenoptera is highly modified, and it was thought that a thorough survey of the flightless forms might reveal that the process of modification had been different among different groups and might have classificatory value. Though the discovery of evidence bearing upon classification was the chief aim in view, it was evident that a number of other aspects of the subject could be investigated simultaneously, *e.g.* what changes in thoracic structure are always associated with loss or shortening of the wings, and which are the more important special types of modification. Lastly rough estimates have been made of the number of wingless and short-winged species known among the various groups of Hymenoptera. These estimates are necessarily very approximate as many groups have not been monographed. In those groups for which no comprehensive systematic works exist, it has been necessary to use indirect methods of calculation to arrive at an estimate of the percentages of wingless and short-winged species. It may be remarked that a large number of the species commonly referred to in the literature as wingless are not so, but have more or less well-developed wing-stumps. The term " short-winged " is obviously an arbitrary one; there is no room for doubt when the wings are reduced to half the normal length or less, but where the reduction is not as great, one author might mention that the wings were shortened while another might make no comment. Similarly it is not possible to say at what point in the process of reduction the wings become too small for flight; it is possible that the muscles of flight become reduced to an extent that makes flight impossible, before the wings themselves become too small. However, I have made use of the term " flightless " to include both the terms " short-winged " and " wingless."

II. *General considerations governing the drawing of conclusions about affinities from studies of the wingless thorax.*

In drawing conclusions about the affinities of any groups from a consideration of the thoracic structure of the flightless forms in those groups, there are certain guiding principles. First, it is usually only one sex of a species that is flightless, in the majority of cases the female. Therefore, differences between the winged and non-winged thorax, due to an initial sexual dimorphism and unconnected with the powers of flight, have to be allowed for. Such an allowance can only be properly made in those groups in which there are species that have both sexes winged as well as species with wingless forms. The Tiphiidae illustrate this question; in the wingless females the mesopleura are extraordinarily prominent, but examination shows that the fully

winged females also have the mesopleura more prominent than those of their males. Thus the very prominent condition of the mesopleura of the wingless females in this family is not entirely an effect of the loss of wings.

Secondly there is the question of variation within a group such as a family. Such variation is, broadly speaking, of two kinds. The first is due to the normal structural diversity found within the limits of a family and classed as generic, specific, and other degrees of difference. In order to allow for this kind of variation when comparing the structure of the wingless thorax of two or more families, one seeks for characters that are common to the wingless thoraces of all members of any one of the families, leaving out of consideration most of the characters that are of less than family rank. The second kind of variation is that which is due to differing degrees of thoracic modification; thus in two closely allied genera, e.g. *Hemiteles* and *Gelis* (= *Pezomachus*) (ICHNEUMONIDAE), there are all stages from the fully winged to the completely apterous condition with corresponding thoracic modifications. It is not detailed similarity of thoracic structure which connects together members of such a series, for each has a thorax that is different in a greater or lesser degree from the other members of the series; what does connect them is the single process of modification that is at work in all of them; they all display the same tendencies, only some have proceeded farther along the path of modification than others. Therefore it is largely true to say that the most highly modified forms are the most typical, for they display most clearly the tendencies common to all members of the series.

The inference from the earlier part of the foregoing paragraph is that one should, where possible, avoid making a detailed comparison between one species from one family and one species from another. If this is done there is a danger that characters which are of less than family rank will be used in the comparison as if they were family characters. Where the type of wingless thorax characteristic of one family can be compared in detail with that characteristic of another, one finds the close similarity of type that is seen in the THYNNIDAE and TIPHIIDAE. The comparison of the types of modification that have acted in different groups may be made between groups more widely separated than families, for it can also be applied where the groups are too dissimilar to show the likeness in details that the other method of comparison requires. Thus on the whole comparison of types of modification is more valuable than comparison of types of wingless thorax characteristic of groups; in other words, the method of comparing how the observed thoracic structure of groups has been brought about, *i.e.* what has happened, is more valuable than the method of comparing what exists. Nevertheless the method has to be used with caution, for while a close similarity in the type of wingless thorax characteristic of two or more groups probably indicates a real affinity between them, this is not necessarily the case where only the process of modification has been the same. It seems that the modes of modification possible are strictly limited in number, and this is to be expected, for the proximate cause of modification (loss of flight) is the same in every case, and some of the results achieved are always the same, *e.g.* reduction in size of the mesothorax. Thus if in two groups the pronotum always fuses with the mesonotum in the wingless forms, this in itself is not enough to indicate affinity between the two groups; it is necessary to find quite other points of structure that they have in common, before one can feel certain that there is a real affinity between them.

So far as possible I have been guided by these principles. Whenever the thoracic structure has appeared to indicate affinities between groups, an

endeavour has been made to substantiate this by finding other characters shared by the groups. In doing so one is handicapped to some extent by the impossibility in a short study of making certain that such characters do in fact occur in every member of the groups in question. However, the risk of falling into error on this account can be greatly minimised by choosing characters which appear to be fundamental.

III. *The structure of the normal thorax in the clistogastrous Hymenoptera.*

In the previous paragraphs emphasis has been laid upon the importance of understanding the processes of modification that have occurred in the flightless thoraces, and to do this they must be compared with the fully winged types from which they have been derived. Consequently a brief description of the thoracic structure of the winged clistogastrous Hymenoptera will be necessary; as far as I am aware there are no wingless forms among the Chalastogastra. The work of Snodgrass (1910) has been followed here, with certain modifications where the mesonotum is concerned, and much the same lettering has been adopted for the figures. In his work, Snodgrass shows how the clistogastrous thorax has been derived by specialisation from the chalastogastrous type, and it will be unnecessary to enter into that here.

Fig. 57 is a lateral view of the thorax of a Pompilid, *Hadropompilus montanus* Arn., which is an unspecialised type.

Prothorax.

The prothorax consists of two very distinct parts and is much modified. The ventral part or " propectus " is formed of the two " propleura " each of which is composed almost entirely of the " proepisternum " (Eps_1), the " proepimeron " being much reduced. The propleura meet along the median ventral line, and posterior to them and usually much hidden between the first coxae (Cx_1) lies the small " prosternum " (S_1). Anteriorly the propectus supports the head, usually sharing this duty with the " pronotum "; posteriorly the first coxae are attached to it. For figures of the propectus see Snodgrass (1910, fig. 17, etc.). The dorsal part of the prothorax is the pronotum (N_1) which has been largely subordinated in function to the mesothorax.

Mesothorax.

The mesothorax is the largest part of the thorax, for it is chiefly concerned with the working of the fore-wings which are the main organs of flight. The notal region (dorsal) will be considered last, for it is the most complex part and requires special mention. The " mesosternum " (S_2) is usually continuous with the two " mesopleura " (Pl_2), but sometimes the " sterno-pleural " sutures (q) are visible. The sterna hardly concern one here, so that it will be sufficient to recognise the existence of the pro-, meso- and metasterna without bothering about their subdivisions, especially as these are not often well marked. But it is necessary to be able to recognise the posterior limits of the mesosternum, for it is easy in some species to include part of the metasternum in the mesosternum. Figs. 5 and 6 show the ventral thoracic aspects of the male and female of *Mutilla europaea* L.; the meso-metasternal suture is that which passes close to the posterior border of the second coxal pits; the large " furcal " pit (Fp) is also close to the suture. Each mesopleuron consists of episternum (Eps_2) and epimeron (Epm_2), but the latter is usually very narrow or suppressed, though in many Chalcidids it is as large as the episternum, as is

the general rule amongst the TENTHREDINIDAE. The suture separating the two is the " pleural suture " (Ps_2) and when fully developed it runs from the middle of the base of the second coxa to the anterior wing process (Wp_2). The mesopleuron (strictly the episternum only) may be divided into dorsal and ventral portions by a suture (r_2). An anterior region may be differentiated from the mesopleura and the mesosternum by a more or less well-marked suture; this region is the " prepectus " ($Ppct_2$). Sometimes as in the TIPHIIDAE and THYNNIDAE, and as in *Microterys* (Chalcidoidea) (Snodgrass, 1910 : fig. 43), the sternal portion of the prepectus is missing.

Turning now to the notal region of the mesothorax (figs. 20, 43, etc.) : the " mesonotum " is usually considered to be divided into two major regions—an anterior " scutum " (Sct_2) and a posterior " scutellum " (Scl_2). Snodgrass (1910, 1935) has shown, however, that the scutum and scutellum as usually recognised in the Clistogastra are not homologous with those of other orders of insects, nor with those of certain of the least modified Chalastogastra. In the Clistogastra there is a strong transverse suture on the mesonotum (the " transcutal suture " k), which is usually regarded as that separating the scutum from the scutellum, but in fact, as Snodgrass has shown, this suture is secondary (it is only feebly developed in most Chalastogastra) and lies in the true scutum. The true " scuto-scutellar suture " (Vnr), which is homologous with that of other orders, is posterior to the transcutal suture, k, and forms the posterior boundary of the " axillary region " (ax) (Snodgrass, 1935 : fig. 101). This axillary region is not given any special name by Snodgrass. Tulloch (1935) does not recognise that it is morphologically part of the scutum, and regarding it as cut off from the scutellum, calls it the " prescutellum." When this region is much constricted medially but is large laterally so that it forms two areas antero-lateral to the scutellum (as in Chalcidids), these areas are called the axillae by hymenopterists; this term is unfortunate as it is more properly applied to the articulatory sclerites in the bases of the wings. The term " postscutum " would indicate the morphological affinity of the region, but it has the disadvantage of running counter to common usage and of conveying the impression that the area is of equal status with the primary divisions of the mesonotum: the " prescutum," " scutum," " scutellum " and " postscutellum." It might be conveniently called the " axillary region " and when it is divided into two lateral areas the term " notal axillae " would serve to avoid confusion with the " alar axillae." So long as it is recognised that the transcutal suture is not homologous with the scuto-scutellar suture of other orders, there is no harm in continuing to treat it as the dividing line between the scutum and scutellum; indeed it would be difficult to do otherwise, for the true scuto-scutellar suture is often very vague.

The " prescutum " (Psc_2) is an area of somewhat variable shape and degree of development; in its simplest and most clearly developed condition as seen in many sawflies, it is a triangular area occupying a median anterior position on the mesonotum. The base of the triangle is formed by the anterior edge of the mesonotum, and the sides by the furrows known as the " notauli " or more correctly " notaulices " (No); these arise from the anterior edge of the mesonotum and converge and meet posteriorly, forming the apex of the prescutum. Most frequently, however, in the Clistogastra the notaulices, though nearly always convergent in a greater or lesser degree, do not meet before they reach the transcutal suture (figs. 46, 48, 54); in such cases the prescutum by definition extends back to the transcutal suture. Though Snodgrass (1910) used the term prescutum in the sense defined here, he now considers (1935) that this notal

area of the Hymenoptera is not homologous with the prescutum of other insects, and restricts the use of the term prescutum in the Hymenoptera to a narrow band round the anterior edge of the scutum in some sawflies.

The " scutum " frequently bears laterally a pair of " parapsidal furrows " (Pf) which mark off a pair of lateral areas of the scutum, the " parapsides " (Pa). The parapsidal furrows and notaulices are of considerable importance in the taxonomy of the Hymenoptera and may well be found to have greater value in the future; consequently it is most necessary that they should be correctly identified and not confused with one another as has frequently occurred in the past. Tulloch emphasised the necessity of correct identification and has discussed the matter in a separate paper (1929). As he points out, the confusion arises when only one of the pairs of furrows is present, for unless the normal positions of the furrows are well understood, it may be difficult to decide which of the two a single pair may be. Tulloch points out that the notaulices are median to the parapsidal furrows, and even when the notaulices alone are present they are seldom as wide apart as the parapsidal furrows; furthermore the notaulices usually commence at the anterior border of the scutum and often become fainter posteriorly, while the reverse is true of the parapsidal furrows. However, the foregoing general rules have exceptions and difficult cases seem quite often to be met with, but I believe that the following point about the parapsidal furrows will help to solve some of these. Laterally the scutum has a longitudinal ridge, sharp or blunt, which runs just dorsal to the tegula. This ridge (R) is called by Tulloch (1935) the " parascutal ridge " and in my material the parapsidal furrows nearly always commence at, or close to, the point where the transcutal suture crosses this parascutal ridge (figs. 20, 28, 43, 48, 52, 54). There is another structure connected with the parascutal ridge that requires to be mentioned; this is a ridge, Axl in the figures, which crosses the lateral part of the axillary region. When fully developed it commences antero-dorsally at the point where the transcutal suture crosses the parascutal ridge and runs postero-ventrally until it cuts the posterior margin of the mesonotum. Sometimes only the posterior portion appears to be present, and in the honey bee this ridge does not seem to be developed at all. Often there is a deep excavation opening posteriorly, situated at the ventral end of this ridge. Snodgrass (1910) makes no mention of this ridge; Tulloch (1935) calls it the " axillary ridge " which appears to be a useful term, and it is clearly shown in some of his figures, especially those of *Paraponera clavata* (Fab.) (pl. 8, figs. 1 and 3). The only portions of the mesonotum that still remain to be mentioned are the " mesopostnotum " or " mesopostscutellum," and the mesothoracic " phragmata." The mesopostnotum, which is posterior to and continuous with the scutellum, is plainly visible in most Chalastogastra, but seems always to be invaginated and hidden beneath the " metanotum " in Clistogastra. The phragmata are internal structures to which the muscles of flight are attached. The anterior or " prephragma " is connected to the anterior border of the mesonotum; the posterior or " postphragma," which is usually very much larger than the anterior one, and is shaped like the upper mandible of a bird's beak, is connected to the mesopostnotum.

Metathorax.

The metathorax of the Hymenoptera is very much smaller than the mesothorax. For purposes of description one may return to the figure of *Hadropompilus montanus* Arn. (fig. 57). The metanotum (N_3) is a single transverse band to which the hind-wings are attached; the " metapostnotum " (PN_3) is well

developed in Pompilids (fig. 57), usually it is much invaginated and fused with the " propodeum," but is generally distinguishable laterally. The " metapleuron " (Pl_3) is always separated by a suture from the metanotum, but is usually continuous with the metapostnotum; it is separated from the " mesopleuron " (Pl_2) by the " meso-metapleural suture " (B), which commences at the posterior side of the base of the second coxa and runs antero-dorsally to the base of the hind-wing. The metapleuron shows no sign of a division into episternum and epimeron, though it is so divided in the Chalastogastra; but it is often divided into dorsal and ventral portions as in the mesopleuron. The suture (r_3) which thus divides the metapleuron seems always to pass through a pit (Edp) which marks the position where a part of the thorax has been invaginated to form some of the internal skeleton of the thorax. This " endophragmal " pit is often of use in marking the approximate position of the suture separating the metapleuron from the propodeum when this has been lost, as often occurs. The pit is usually on the " metapleural-propodeal suture " (C), but in *Rhopalosoma guianense* Schulz it is on the suture dividing the metapleuron, but not on the metapleural-propodeal suture. The " metasternum " (S_3) has already been mentioned; it may or may not be separated by a suture from the metapleuron.

Propodeum.

The " propodeum " of the Clistogastra is morphologically the first abdominal segment which has become transferred to the thorax and is intimately fused with it; it consists entirely of the tergum, the sternal portion having become desclerotised. As Snodgrass (1910) points out, lack of knowledge of the true nature of the propodeum in the past has led to considerable confusion in the naming of the metanotum, metapostnotum and propodeum. The propodeum is frequently called the metathorax, while the metanotum is called the postscutellum of the mesothorax. The propodeum has also been called the " median segment " and (by myrmecologists) the " epinotum."

IV. *Landmarks on the thorax.*

In flightless forms with a very modified thorax the sutures may be much obliterated and other landmarks have to be used in order to interpret the structure. The following are some of the more useful landmarks. The pronotal, metathoracic, and propodeal spiracles are important. In winged forms the pronotal and metathoracic spiracles are concealed; the former beneath the postero-dorsal angles of the pronotum, the latter beneath the bases of the hind-wings. In wingless forms the pronotal spiracles are nearly always visible and serve to mark the junction between the dorsal and lateral posterior margins of the pronotum, even when the pronotum has fused with the mesonotum. The metathoracic spiracle is always exposed in wingless forms, but may be so reduced as to be no longer visible; its original position is in the membrane between the meso- and metapleura, but it sometimes has the appearance of belonging to the metapleuron (many worker ants) and it is convenient to call it the metathoracic spiracle. In many forms it is at the dorsal termination of the meso-metapleural suture (this is of use in the MUTILLIDAE) and with very few exceptions it is always on the line of junction of the dorsum and pleura. The propodeal (or true first abdominal) spiracle is nearly always easily visible, though not very constant in position. This inconstancy is sometimes useful, for in many wingless forms the propodeum becomes larger and by comparing the position of the propodeal spiracle in the

winged and wingless forms, it is often possible to say in which part of the propodeum the greatest amount of growth has occurred. The endophragmal pit of the metapleuron (Edp) (see page 373) is often useful in locating the approximate position of the hind margin of the metapleuron, for the metapleural-propodeal suture is very commonly lost in wingless forms. The meso-metapleural suture is nearly always visible and forms a useful guide line; its dorsal termination marks the position of the metathoracic spiracle and approximately the position of the point of junction laterally of the meso- and metanotum.

V. *Thoracic modifications common to all flightless forms.*

Loss of flight always leads to reduction in the volume of the mesothorax; modifications of the prothorax, metathorax and propodeum may or may not occur. The large and complicated mesonotum is almost entirely concerned with the function of flight and it contains the large longitudinal muscles of flight, besides serving as the dorsal attachment for the dorso-ventral muscles of flight which lie on either side of the longitudinals. The latter are connected anteriorly and posteriorly to the pre- and postphragmata of the mesonotum and it is probable that these phragmata are always the first sclerotised parts to undergo reduction on loss of the power of flight (see page 439). The mesonotum is the first part of the thorax to show modification; first it becomes less convex; *i.e.* in lateral view it becomes depressed compared with the unmodified condition. Next it usually becomes shorter and narrower. The rest of the mesothorax shows changes of the same kind, but less marked than those of the mesonotum. In many forms in which the wings are reduced to mere stumps, modification may proceed no farther than a reduction in volume of the mesothorax with perhaps a partial obliteration of such features as the parapsidal furrows. Thus the only modification common to all flightless forms is some degree of reduction in volume of the mesothorax and, in succeeding pages, when a wingless form is said to have the thorax almost unmodified, it is meant that very little more than this has occurred. Since the greatest changes occur in the dorsum of the thorax, I have paid more attention to it than to other parts, and the majority of the figures are dorsal views.

While it is comparatively easy to see when some part of a wingless thorax has undergone reduction in size, it is often much less easy to be certain when the opposite has occurred. Increase in size of the pronotum and propodeum is characteristic of the thorax of some wingless forms, and when the increase is considerable there can be no doubt about it, but slight increases in size are difficult to detect because there is no standard for comparison. First of all, increases in size of some part usually occur only in the more modified thoraces, where the parts are of abnormal shape as well as size; this makes comparison with the normal thorax difficult. Any such comparison is more complicated because the two sexes of species in which one sex is wingless are usually very different in size so that direct comparison of the size of the part in the winged and wingless thorax is seldom possible. Similarly it is generally useless to express the dimensions of the part which is suspected to have become larger, in terms of the dimensions of some other part such as the head, for this also will usually display considerable sexual dimorphism. It is useless to say that the part in question is larger in comparison with the rest of the thorax than it is in the winged thorax, for much of the wingless thorax will have become smaller, so that the part would be larger by comparison, even if it did not alter in size. It is therefore unwise to try to make any decision about doubtful cases; where it is perfectly

obvious that a part has become larger I have said that the part is " relatively larger in the wingless form," meaning that if the winged and wingless thoraces were of about the same size the part would be larger in the wingless thorax.

VI. *The wingless thorax among the various groups of Hymenoptera.*

The main groups in which short-winged or wingless forms occur are the MUTILLIDAE and MYRMOSIDAE and their allies; the THYNNIDAE, the TIPHIIDAE and the Bethyloidea and POMPILIDAE. These all belong to Ashmead's Vespoidea and with the FORMICIDAE complete the Aculeates. Among the Terebrantia, the Proctotrupoidea, the CYNIPIDAE, the Chalcidoidea, the Ichneumonoidea and BRACONIDAE contain wingless or short-winged forms.

1. MUTILLIDAE.

I commence with the MUTILLIDAE because it is a family containing 3500 or more species, so that a large amount of material can be studied; also all the females are wingless and have a very highly modified thorax. Thus by studying this family first it is possible to form some idea of the normal range of variation in the morphology of the wingless thorax of a single family. The study of other groups containing wingless forms can then be undertaken, knowing that they will be unlikely to display any condition more simplified and at the same time more specialised than that of the MUTILLIDAE.

As this is the first group to be considered, the modifications of the female thorax are discussed in rather more detail than in succeeding groups. Figs. 1 and 2 show dorsal and lateral views of the thorax of the male of *Mutilla europaea* L. Figs. 3 and 4 are the corresponding views of the female. It will be seen that the thorax of the male is of a normal aculeate type so that it is unnecessary to describe it in detail and the female thorax can be discussed by comparison with the figures of the male.

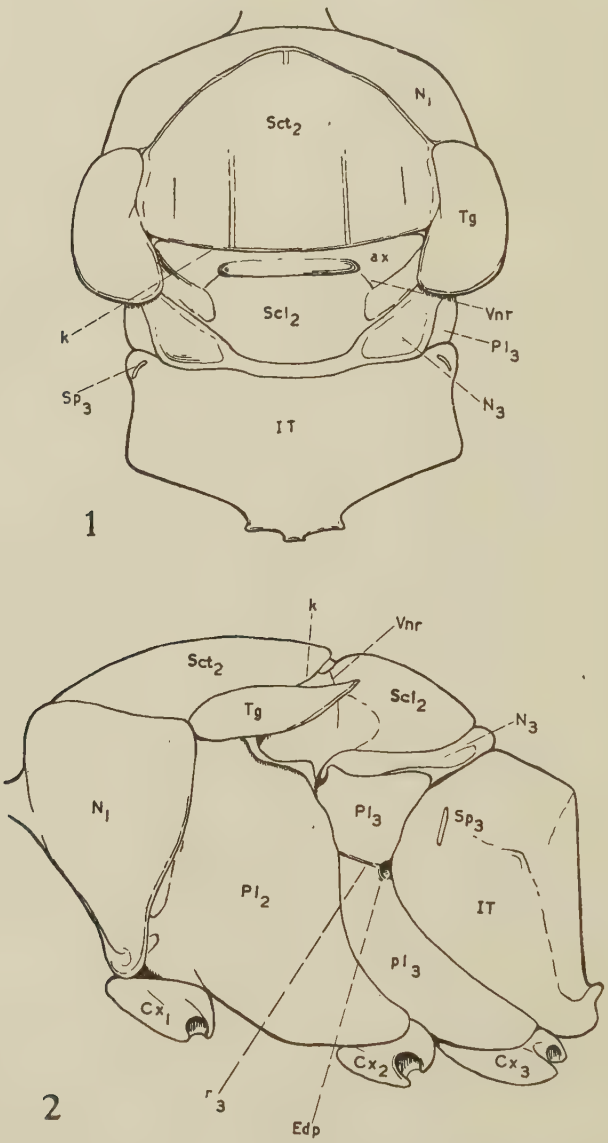
General condition of the female thorax compared with that of the male.

The thorax of female Mutillids is strongly fused into a single box-like whole by great reduction or complete obliteration of sutures. The dorsum in particular forms a single convex surface, often with no signs of any sutures at all. There is considerable reduction in volume of the female thorax compared with that of the male; this is largely due to a reduction in total length, mostly of the mesothorax, and also to a narrowing of the sterna and to a concave condition (best developed in the more specialised forms) of the pleura.

Detailed condition of the female thorax.

Dorsal :—The dorsum forms a single convex surface, from the anterior edge of the pronotum, exclusive of the " neck " region, to the back of the propodeum, shorter than the corresponding length in the male; for example, two specimens of *Mutilla europaea* L. measured along the length defined were, male 6 units, and female 5 units. Usually the periphery of the dorsum is fairly well defined, the pleura and the dorsum meeting (unlike the male) more or less at right angles. Sometimes the junction of the pro- and mesonotum is indicated by a change in the sculpturing, hardly to be called a suture; *e.g.* some species of *Dasylabris*. When this line is visible it is emarginate as in the male but much less so. The suture most frequently indicated upon the dorsum is one just anterior to the propodeal spiracles; as with the pronotal suture it is indicated by a change in the sculpturing. It is difficult to be quite certain which this

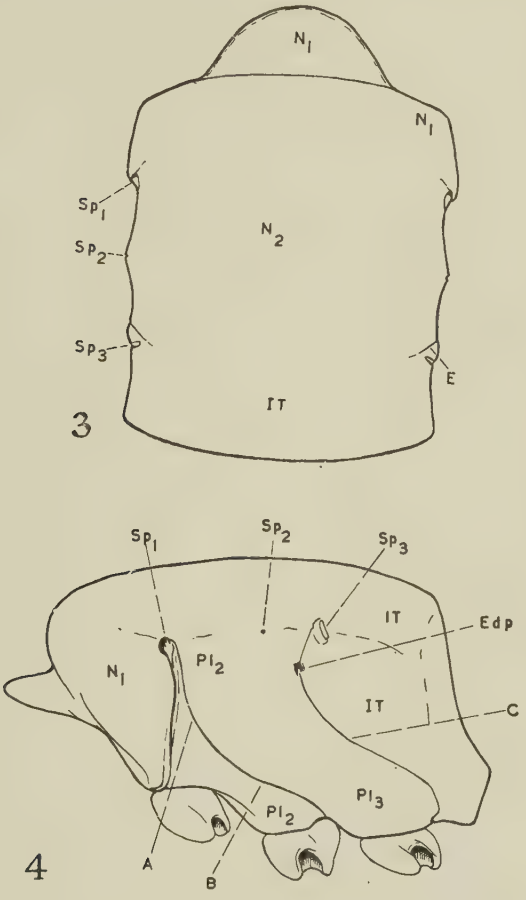
suture is, but examination of some of the wingless male Mutillids makes it very probable that it is always the one between the metapostnotum and propodeum and represents, at least medially, all that remains of the meta-



FIGS. 1–2.—*Mutilla europaea* (MUTILLIDAE), 1, ♂, dorsal; 2, ♂, lateral.
For explanation of symbols see p. 446.

postnotum. Fig. 7 shows the dorsal aspect of the wingless thorax of the male of *Myrmilla capitata* (Lucas). The suture between the metanotum (plus metapostnotum) and propodeum is stronger than that between the metanotum

and mesoscutellum and it seems that in the female Mutillids the metanotum probably fuses with the mesoscutellum. This is borne out by the appearance of the thorax in other wingless male Mutillids; e.g. *Myrmilla chiesii* (Spin.), *Odontotilla bidentata* (André) and *Brachymutilla androgyna* André. In the last-named species the thorax of the male is quite as modified and shows just as much fusion of parts as that of many female Mutillids; it is, however, rather less modified than that of its female. In some female Mutillids there is a

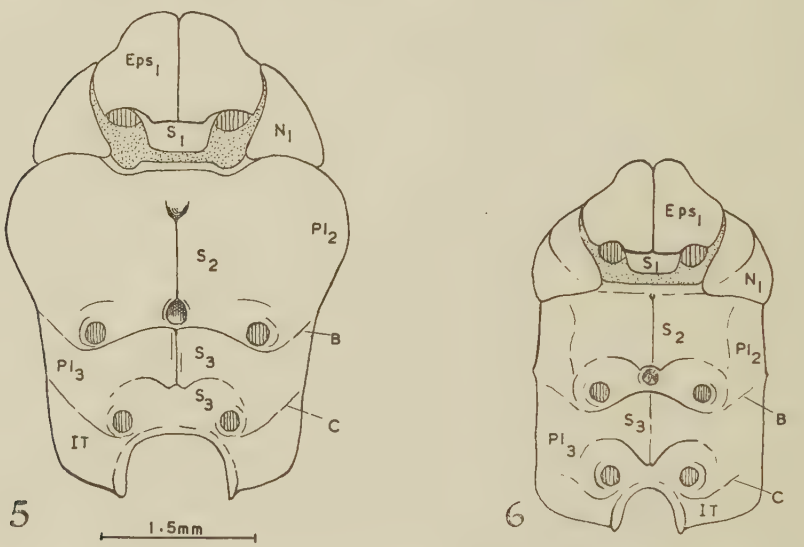


FIGS. 3–4.—*Mutilla europaea* (MUTILLIDAE), 3, ♀, dorsal; 4, ♀, lateral.

second suture on the dorsum anterior to the metapostnotal-propodeal one just discussed; this arises laterally from the point where the meso-metapleural suture meets the metathoracic spiracle and passes postero-medially to fuse with the metapostnotal-propodeal suture. By comparison with fig. 7 it is evident that this is the suture that divides the metanotum from the fused metapleuron and metapostnotum. In many female Mutillids in the posterior half of the thorax there is a median dorsal scale or tooth called the " scutellar " scale; since the metapostnotal-propodeal suture appears to pass close to the posterior side of the base of this scale, it seems more likely that this scale belongs

to the metanotum than to the scutellum. Mickel (1938), in giving the taxonomic characters of the females of *Timulla*, says that " in many species there is a well-defined transverse groove or suture immediately anterior to the scutellar scale; in others this mesonotal-scutellar suture, as I have called it, is indistinct or entirely absent." If I am right in supposing that the scutellar scale is anterior to the metapostnotal-propodeal suture and belongs to the metanotum, then this suture mentioned by Mickel is presumably that between the meso- and metanota.

Lateral :—Of all parts of the thorax in Mutillids, the pleura are the most worth studying, because the sutures are usually at least partially visible, so that it is easier to estimate what changes have occurred. The pleura tend to become concave and polished; this condition is developed in all degrees. The most important change is the great reduction in size of the mesopleuron. This



FIGS. 5–6.—*Mutilla europaea* (MUTILLIDAE), 5, ♂, ventral; 6, ♀, ventral.

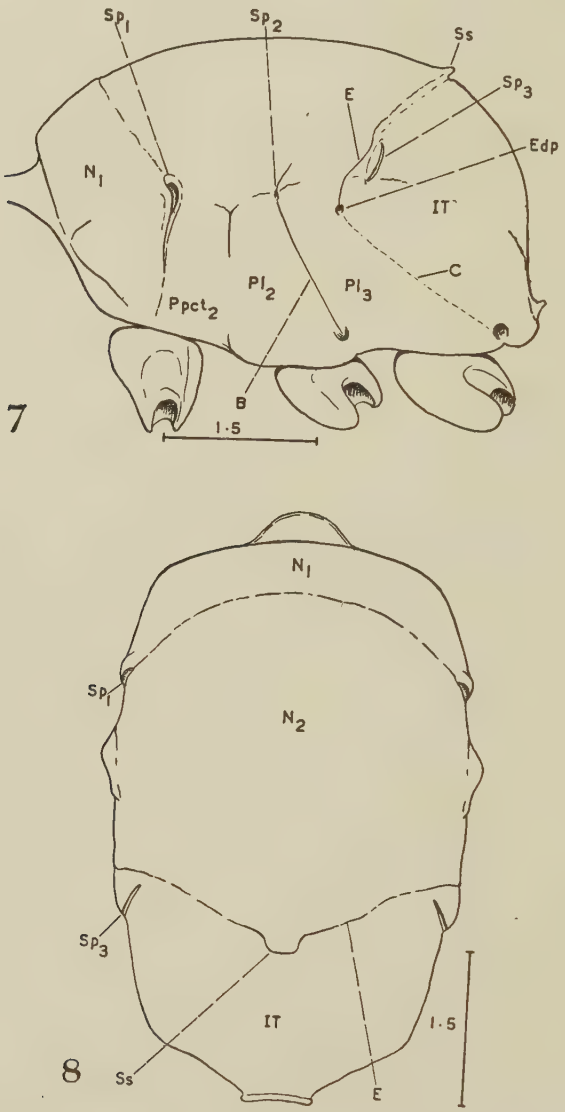
changes from a bulging structure in the male to a concave one in specialised female thoraces, such as those of *Mutilla*. To express the change in size numerically it is best, for reasons which will be apparent later, to measure the length of the mesopleuron from its hind margin just above the second coxa to its anterior margin at the ventral posterior angle of the pronotum. In a male of *Mutilla europaea* L. this length was rather more than 3 units, and in a female rather less than 2. This reduction causes the first and second coxae to be much closer together than in the male. When the mesopleuron is concave it is smooth and only slightly punctured, instead of rugosely punctured as in the male; when not concave the punctures also remain strong. The mesopleuron shows no sign of division into dorsal and ventral parts. The metapleuron is much as in the male; sometimes the division into dorsal and ventral parts is visible and as in the male takes its origin from the endophragmal pit. The area of the propodeum is about the same as that of the male; the pronotum is also of about the same area as in the male and in most cases the lateral suture,

though evident, is more or less fused up. The dorsal angles of the pronotum are considerably reduced so that the pronotal spiracle is much more obvious than in the male. Usually the female has a somewhat imperfectly defined prepectus which is hardly visible in the male (see pp. 381–382).

Ventral (figs. 5 and 6) :—The only noteworthy difference here is the reduction in size of the mesosternum; much of the reduction in length occurs in front of the foremost of the two furcal pits; in addition, in the females of *Mutilla europaea* L. and other species, this area is concave instead of convex as in the males.

Having dealt with the general condition of the female thorax of the Mutillidae, the range of modifications exhibited by the thorax of the females may be considered. The thoracic structure of the females of certain genera is more primitive than that of others, for it has departed less from male condition. *Dasylabris* (figs. 7 and 8) and *Stenomutilla* are examples. The mesopleuron of the females is convex; in *Stenomutilla* it is rounded much as in the male, in *Dasylabris* it projects wedge fashion. The meso-metapleural suture is normal, running from above the second coxa to the metathoracic spiracle, which is usually visible in the female, but sometimes very small and then only seen after some experience. The postero-lateral suture of the prepectus, called hereafter the " prepectal suture," is visible in *Stenomutilla*, but in *Dasylabris* is indicated by a line of long hairs which project at right angles from the thorax; this line is placed just in front of, or on the edge of the mesopleural wedge. In these two genera the mesopleuron is punctured as in the male, particularly in *Stenomutilla*. In *Dasylabris* the anterior and posterior sutures of the metapleuron are clear, and the division of the metapleuron is sometimes visible; the corresponding sutures of *Stenomutilla* are mostly obliterated. The anterior part of the mesosternum, including the prepectal portion, is well developed compared with *Mutilla*, *Smicromyrme* and allied genera. These last two genera come somewhere near the opposite extreme and show very well a curious secondary condition of the meso-metapleural suture, the development of which can be traced through successive genera. In *Mutilla*, *Smicromyrme*, etc., the mesopleuron has become concave and is hardly punctured, while the anterior portion of the mesosternum is very small. The dorsal portion of the meso-metapleural suture (fig. 4) appears to have been shifted very much anteriorly, for it starts above the second coxa, but apparently ends in the hind margin of the pronotal spiracle; while no suture runs up to the metathoracic spiracle. Examination of other genera provides the explanation. The meso-metapleural suture bends anteriorly until it meets the prepectal suture. If then, as in many specimens of *Mutilla europaea* L., the meso-metapleural suture dorsal to its point of fusion with the prepectal suture is lost, and the prepectal suture, ventral to this point of fusion, is also lost, the meso-metapleural suture then appears as described above (fig. 4). Intermediate conditions occur so that the process of modification can be followed fairly completely. At the beginning of the series are unmodified forms such as *Dasylabris merope* (Sm.) (fig. 7) which has already been shown to be primitive for other reasons. Here the meso-metapleural suture pursues the normal straight course from the base of the second coxa to the metathoracic spiracle. The dorsal termination of the prepectal suture is widely separated from the pronotal spiracle. There appear to be only a few other genera that display this unmodified condition of the meso-metapleural suture; I have observed it in *Squamulotilla*, *Brachymutilla*, and *Stenomutilla*, but none of these, except *Stenomutilla*, is as primitive in other respects as *Dasylabris*.

Some of the species of *Ephutomorpha* may be taken, perhaps arbitrarily, to exemplify the first step in the series of modifications. Thus in *Ephutomorpha pulchella* (Sm.) the meso-metapleural suture is considerably bent forwards



Figs. 7–8.—*Dasylabris merope* (Mutillidae), 7, ♀, lateral; 8, ♀, dorsal.

and it gives rise to a secondary suture or ridge which meets the dorsum between the metathoracic spiracle and the dorsal termination of the prepectal suture. It is unfortunate that the prepectus is not usually clearly marked dorsally in *Ephutomorpha*, but it generally is sufficiently so to see that its dorsal termination is well separated from the pronotal spiracle. In *E.*

pulchella the metapleural-propodeal suture dorsal to the endophragmal pit is not visible, while the faintly marked suture that divides the metapleuron into dorsal and ventral portions occupies a somewhat secondary position as it meets the meso-metapleural suture only a little ventrally to the metathoracic spiracle. *Ephuta* (*Traumatomutilla*) *sociata* (Sm.) (fig. 9) and *Ephuta capitata* (Sm.) show the next step in the series. In the latter the secondary suture which springs from the meso-metapleural suture no longer runs into the dorsum as in *Ephutomorpha pulchella*, but into the prepectal suture which is very clearly marked and dorsally is widely separated from the pronotal spiracle. In *Ephuta sociata* (fig. 9) the process has gone one stage farther, for the meso-

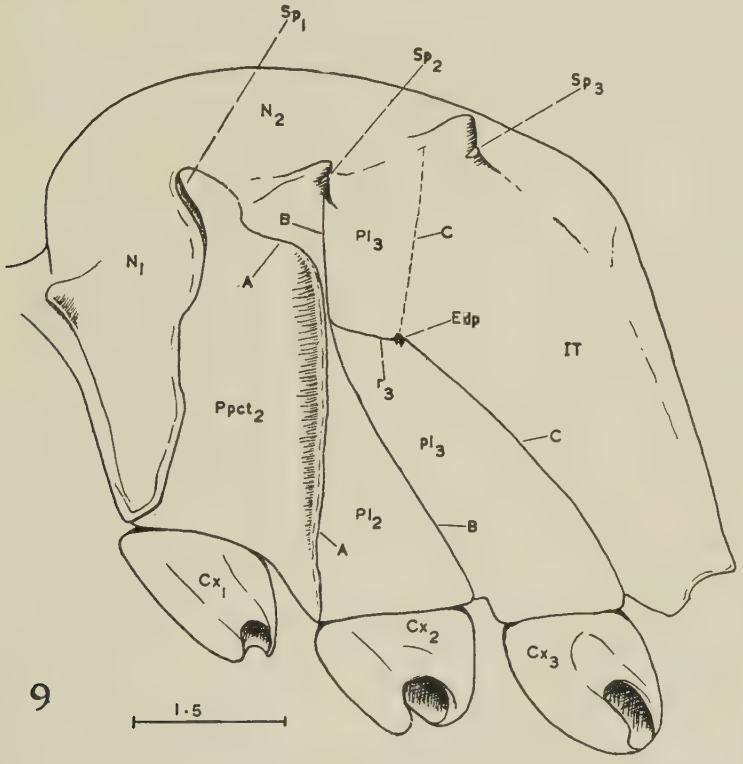


FIG. 9.—*Ephuta sociata* (MUTILLIDAE), ♀, lateral.

metapleural suture approaches the prepectal so closely that the connecting suture is not distinguishable. In this species the prepectus is very wide and the prepectal suture is sharply marked on the summit of an abruptly projecting dorsal ridge; it is widely separated dorsally from the pronotal spiracle. As in *E. capitata*, the metapleural-propodeal suture is faintly distinguishable dorsal to the endophragmal pit. In *E. sociata* the division of the metapleuron is visible and in normal position.

Fig. 10 of *Pycnotilla angonina* Bisch. (subsp. *lualabana* Bisch.) shows the condition directly preceding that of *Mutilla europaea*. The meso-metapleural suture bends strongly forwards from the second coxa and meets the midpoint of the prepectal suture; between this point and the metathoracic spiracle it is

straight and faintly marked. The metapleural-propodeal suture is complete and runs into the propodeal spiracle dorsally; the suture dividing the metapleuron shows a well-marked secondary condition, it forms a strong ridge which curves dorsally and meets the meso-metapleural suture just ventral to the metathoracic spiracle. This secondary condition of the suture dividing the metapleuron occurs in several other species, *e.g. Mutilla parallela* André, *M. cepheus* Sm., *M. astarte* Sm. It may be easily mistaken at first for a portion of the true metapleural-propodeal suture, for it is in a direct line with the rest of the suture ventral to the endophragmal pit, and, like it, is strongly marked; while the true dorsal portion of the metapleural-propodeal suture is faint and easily overlooked. This suture may be certainly identified because it meets the meso-metapleural suture.

By obliteration of the meso-metapleural suture dorsal to its point of fusion with the prepectal, and by loss of the prepectal suture ventrally, the condition seen in *Mutilla europaea* L. and many other species is arrived at. The vertical ridge before the front coxa that is used as a taxonomic character in the

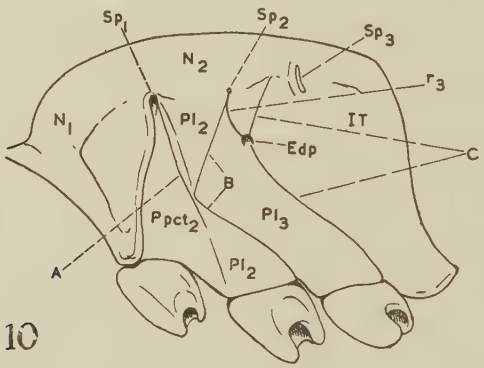


Fig. 10.—*Pycnotilla angonina* (Mutillidae), ♀, lateral.

Mutillidae is probably a part of the prepectal suture, which has a strong tendency in this family to form a ridge rather than a groove. I do not know if these changes in the meso-metapleural suture have any function; possibly changes in the arrangement of the muscles demand alterations in the internal ridges that serve as muscle attachments.

The degree of obliteration of these sutures on the pleura of female Mutillids is very variable, even in individuals of the same species. Thus in some specimens of *Mutilla europaea* the ventral portion of the prepectal suture is not missing, or not entirely missing, and the dorsal portion of the meso-metapleural suture may be very faintly visible. Consequently it is not possible to say that a particular genus is characterised by the presence or absence of a particular pleural suture, as it is likely to be visible in some species of the genus and not in others. It is rather exceptional for the dorsal portion of the meso-metapleural suture, *i.e.* the part between its point of junction with the prepectal suture and the point where it meets the metathoracic spiracle, to be at all clearly visible, but it can be seen in a sufficient number of forms to show that the majority of the Mutillidae are of the specialised *Mutilla* type. Certain genera display this dorsal portion of the modified meso-metapleural suture quite frequently, *e.g. Pycnotilla.*

It has already been hinted that the width of the dorsal part of the prepectus shows some correlation with the degree of modification of the meso-metapleural suture. Broadly speaking, in those forms in which the meso-metapleural suture is unmodified, or not highly modified, the prepectal suture dorsally is widely separated from the pronotal spiracle, while in forms with a fully modified meso-metapleural suture, the prepectal suture ends dorsally in the pronotal spiracle. There are exceptions such as *Ephutomma* in which the meso-metapleural suture is apparently unmodified but the prepectal suture meets the pronotal spiracle. There is a tendency also for the pleura to be more concave and less punctured in forms with a fully modified meso-metapleural suture. It is unlikely that any of these characters of the pleura of female Mutillids have taxonomic value, because they are too variable in degree of development and too often difficult to see; but they are of value in making out the internal phylogeny of the family, especially when considered in conjunction with other morphological characters and with geographical distribution.

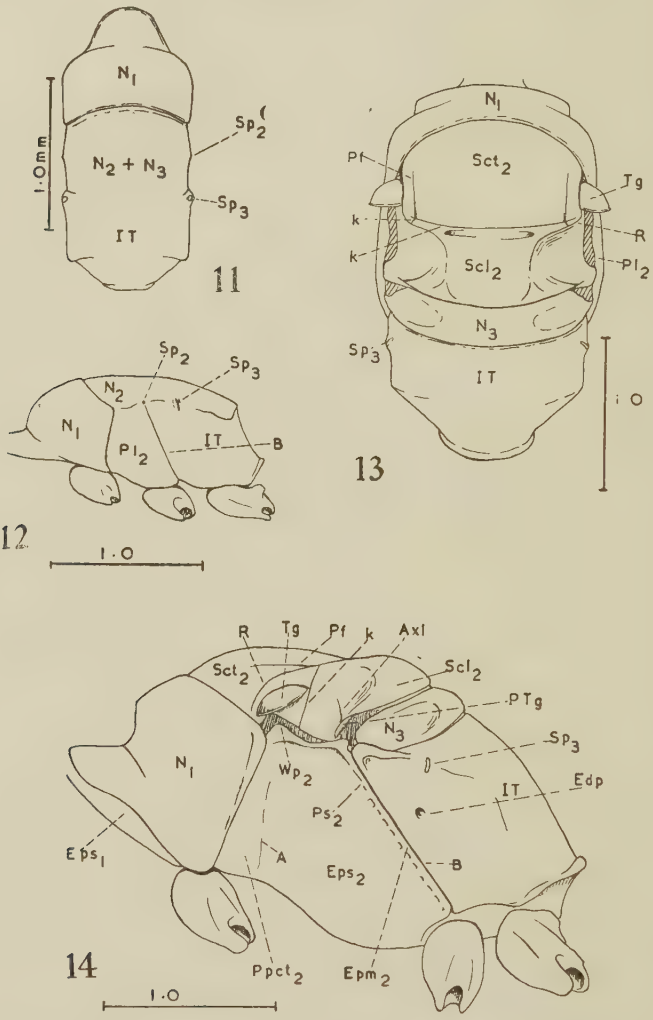
A few other points must be discussed before leaving the MUTILLIDAE. Gynandromorphism has only rarely been recorded; Wheeler (1910) described a good lateral gynandromorph of *Pseudomethoca canadensis* (Blake) and referred to the only earlier record of a gynandromorphous Mutillid; this was a good lateral gynandromorph of *Mutilla europaea* var. *obscura* Nyl. described by Macklin (Dalla Torre and Friese, 1898). Mann (1915) described a mosaic gynandromorph of *Dasymutilla euchroa* (Cock.). These gynandromorphs show plainly the sexual dimorphism of the thorax in the Mutillids.

There are a few genera of MUTILLIDAE in which the males of certain species are wingless as well as the females; *Myrmilla*, *Brachymutilla*, *Apterotilla*, etc. The male of *Myrmilloides grandiceps* (Blake) is short winged. Altogether there are some 20 species distributed among about 5 genera, in which the males are wingless. The thoraces of these males vary from slightly to highly modified, but never so much as those of the more specialised females, and I did not find a modified meso-metapleural suture in any I examined.

In the females of some species of MUTILLIDAE the thorax bears, dorso-laterally, large paired projections (fig. 9) which are often less developed in the males. *Ephutomorpha rugicollis* (Westw.) and *E. ruficornis* (Fab.) show this well; the female of the former has a pair of projections on the anterior lateral corners of the pronotum, a pair at the level of the metathoracic spiracles, and a pair on the propodeum; there is none in the male. In other species the projections are not so large in the males as in the females and the males always lack the second pair which is commonly developed in the females. One might almost say that the females, being wingless, are free to develop these excrescences, while the males cannot do so as they would interfere with the wings. Exactly the same thing occurs in certain genera of ants, particularly *Polyrhachis*, but except for these ants and the Mutillids, apparently not in any other wingless Hymenoptera. The ants are known to be a very ancient group in which the winglessness of the workers is of very long standing and presumably the same is true of the MUTILLIDAE. The whole condition of the female thorax, and in particular the curious modifications of the sutures on the pleura, suggests that the female MUTILLIDAE have been wingless for longer than most other apterous Hymenoptera.

The following are the genera of MUTILLIDAE of which material has been studied; the numerals indicate the numbers of species examined, exclusive of those mentioned in the text:—*Mutilla* 7, *Smicromyrme* 3, *Dasylabris* 4, *Odontotilla* 2, *Labidomilla* 2, *Squamulotilla* 2, *Tricholabioides* 1, *Dasylabroides* 3, *Nano-*

mutilla 1, *Ephutomma* 2, *Tropidotilla* 1, *Pycnotilla* 7, *Ephutomorpha* 20, *Ephuta* 19, *Ephuta* (*Tilluma*) 3, *Ephuta* (*Traumatomutilla*) 4, *Dasymutilla* 9, *Pseudomethoca* 3, *Atillum* 1, *Hoplomutilla* 1, *Rhoptromutilla* 2, *Odontomutilla* 3, *Dolichomutilla* 3, *Lobotilla* 2, *Trogaspidia* 8, *Glossotilla* 2, *Mimecomutilla* 1,



Figs. 11–14.—*Myrmosa atra* (Myrmosidae), 11, ♀, dorsal; 12, ♀, lateral; 13, ♂, dorsal; 14, ♂, lateral.

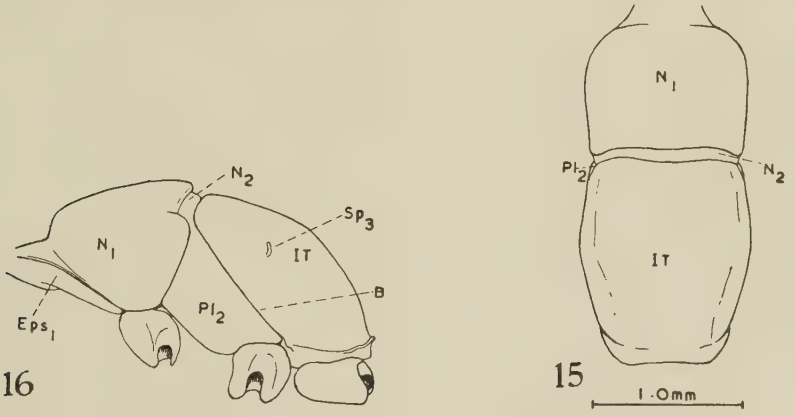
Pristomutilla 2, *Ceratotilla* 1, *Sulcotilla* 1, *Viereckia* 2, *Stenomutilla* 4, *Platymyrmilla* 1, *Myrmilla* 4.

2. Myrmosidae.

The female thorax in this family has a number of points of resemblance to that of the Mutillidae, but it can be at once distinguished by not having the pronotum fused dorsally with the mesonotum.

Figs. 11 and 12, and 13 and 14, show the dorsal and lateral aspects of the thorax of the female and male respectively of *Myrmosa atra* Pz. (*melanocephala* Fab.). Except for the pronotum, which is free both dorsally and laterally, the entire thorax of the female is fused together, the mesonotum, metanotum and propodeum forming one convex surface without sutures. There has been the normal great reduction in size of the mesothorax, but the fusion has not effected much alteration in the relative sizes of the pronotum and propodeum. The metathoracic spiracle occupies the same position as that of female Mutillids and is very small. The meso-metapleural suture is unmodified and pursues a straight course between the base of the second coxa and the metathoracic spiracle. No prepectus is visible. In both sexes the metapleural-propodeal suture is obliterated and the metapleuron is undivided. The propodeal spiracle occupies the same position as in female Mutillids and the pleura, like those of the Mutillids, are concave and lack the rugose puncturing and sculpture of the males.

Material examined:—*Myrmosa atra* Pz. (*melanocephala* Fab.), *ephippium* (Fab.), *frater* Saund., *nigriceps* Saund.



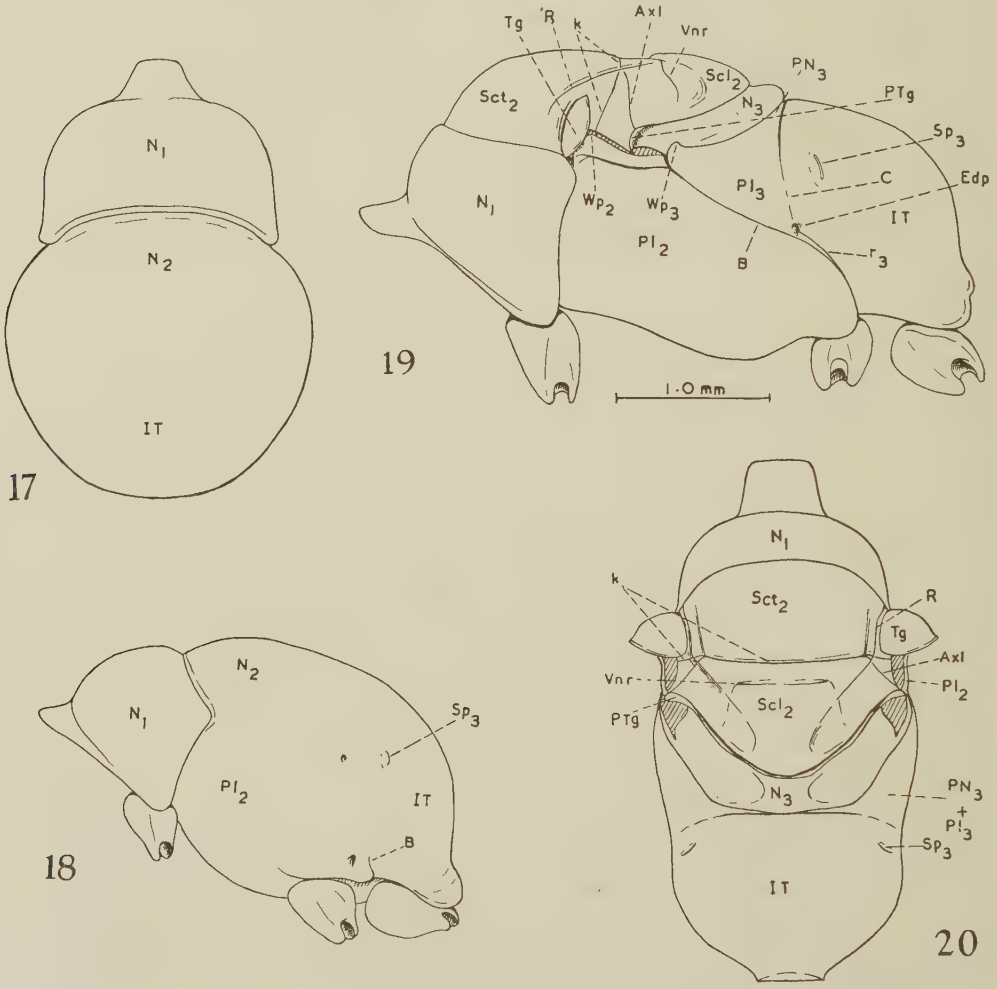
Figs. 15–16.—*Typhoctes guatemalensis*, 15, ♀, dorsal; 16, ♀, lateral.

3. *Typhoctes guatemalensis* Turner.

This genus was established by Ashmead (1899 : 53) to receive the single species *Mutilla peculiaris* Cresson, of which, as far as I know, only the single type specimen is known (figured by Malloch, 1926). *T. guatemalensis* appears to be the only other genuine species of the genus and was also described from a single female specimen which I have examined. Some males have been assigned to this genus, but it is doubtful if they really belong here, as they are apparently very similar to the males of *Chyphotes*, the females of which are very different from those of *Typhoctes*.

Figs. 15 and 16 show the lateral and dorsal views of the thorax of *Typhoctes guatemalensis* Turner, 1910. It is a very peculiar thorax which has been incorrectly interpreted in the past. Dorsally it consists almost entirely of the large pronotum and very large propodeum, but between them is a strongly transverse area, clearly separated by sutures from both of them. This transverse area is the very much reduced and simplified mesonotum; the structure of the side of the thorax proves this, for the meso-metapleural suture is well defined and runs from the base of the second coxa to the posterior margin of

this transverse area and is continuous with the suture separating this area from the propodeum, etc. The metapleural-propodeal suture is not visible and the metanotum has presumably fused with the propodeum, but as the metanotum is always considerably reduced in wingless forms, it is unlikely that it contributes anything but a small fraction to the length of the propodeum, which in consequence can be safely assumed to be relatively much larger than in the male, whatever this insect may be like, provided that it is winged.

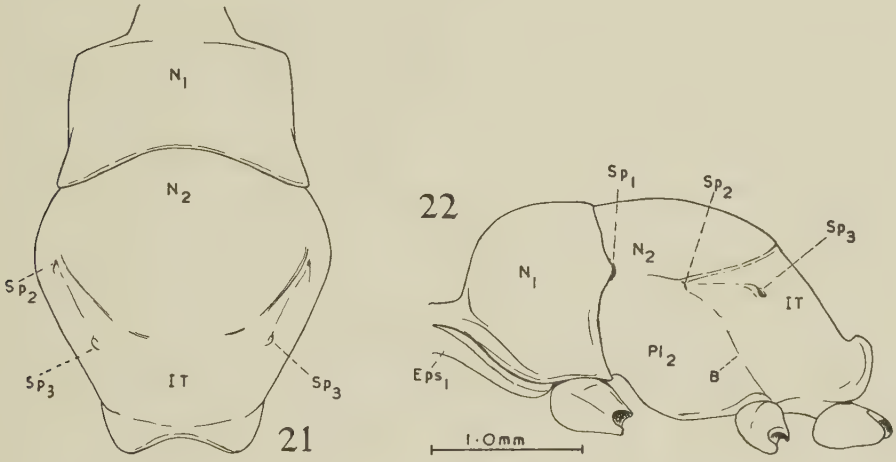


Figs. 17–20.—17–18, *Chyphotes testaceipes*, 17, ♀, dorsal; 18, ♀, lateral; 19, *C. belfragei*, ♂, lateral; 20, ♂, dorsal.

4. *Chyphotes testaceipes* Fox.

Figs. 17 and 18 show dorsal and lateral views of the thorax of the female of *Chyphotes testaceipes* Fox. Figs. 19 and 20 are lateral and dorsal views of the thorax of the male of *C. belfragei* (Blake). The thorax of *C. testaceipes* falls into the same class as that of *Myrmosa*; the pronotum is free, but all the rest

of the thorax is fused into one piece. This posterior part of the thorax is very globular and quite devoid of all sutures except the ventral end of the meso-metapleural suture. The pit anterior to the propodeal spiracle shown in the figure may be the endophragmal pit of the metapleuron; if it is, then it has shifted from the position it occupies in the male thorax (fig. 19); alternatively it might be the metathoracic spiracle, though it does not look like it. Owing to the lack of sutures on the posterior part of the thorax, it is not possible to say what parts of it are formed by the meso- and metathorax and propodeum respectively, but the position of the propodeal spiracle and endophragmal pit, if such it is, indicate that the propodeum has not undergone any marked relative change in size compared with the male thorax. The thorax of the female of *Chyphotes punctatus* Fox, is closely similar to that of *C. testaceipes* and like it lacks any sign of sutures on the posterior part of the thorax. In both species the thorax is heavily punctured and this no doubt contributes to the obliteration of the sutures.



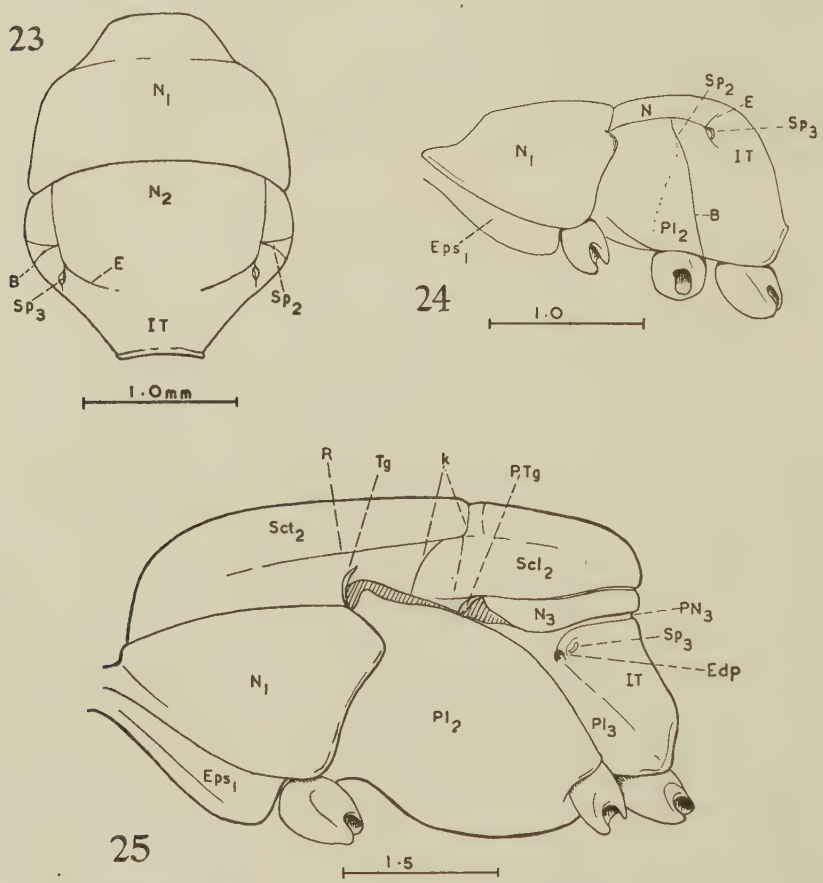
Figs. 21–22.—*Apterogyna nyasana* (Apterogynidae), 21, ♀, dorsal; 22, ♀, lateral.

The chief differences between the thorax of *C. testaceipes* and that of *Myrmosa* are the prominence of the pleura which are in a large measure responsible for the globularity of the hind part of the thorax, and the suppression of all sutures on the pleura; also the fact that the sides of the thorax are no less heavily punctured than in the male.

5. Apterogynidae.

This curious little family is largely African; both sexes are characterised by the first abdominal segment, and to a lesser extent the second also, being nodiform as in ants. Figs. 21 and 22 show the dorsal and lateral aspects of the female thorax of *Apterogyna nyasana* Bisch. The thorax is of the same type as that of *Myrmosa* and *Chyphotes*, having the pronotum free and the rest of the thorax fused together. The only suture on the dorsum is a very faint and incomplete one which appears to be that separating the mesonotum from the metanotum and propodeum, since it arises on each side from the metathoracic spiracle. Laterally, the metathoracic spiracle is visible and the meso-metapleural suture is present though faint. The propodeal spiracle is well developed

and a slight ridge runs anteriorly from it towards the metathoracic spiracle; at least a part of this probably represents the suture dividing the metapleuron from the metanotum. Viewed from above the mesopleura project strongly, but the posterior part of the thorax is less globular than in *Chyphotes*. There appears to have been little or no change in the relative sizes of the pronotum and propodeum compared with the male and evidently the process of modification has been the same as that which has operated in *Chyphotes*. The thorax of the males of *Apterogyna* is quite similar to that of the males of *Chyphotes* (figs. 19



Figs. 23–25.—*Bradynoboenus gayi* (Bradynoboenidae), 23, ♀, dorsal; 24, ♀, lateral; 25, ♂, lateral.

and 20) except for the position of the endophragmal pit of the metapleuron which, as explained later, is rather exceptional in *Chyphotes*.

Material examined :—*A. nigra* Dov., *mutilloides* Sm., *savignyi* Klug, *dorsostriata* André, *pici* André, *olivierii* Latr., *latreillei* Klug, *globularia* (Fab.), *cybele* Pér., *obscura* Bisch.

6. Bradynoboenidae.

This is a very small family of somewhat aberrant insects, natives of South America. Figs. 23 and 24 are the dorsal and lateral aspects of the female

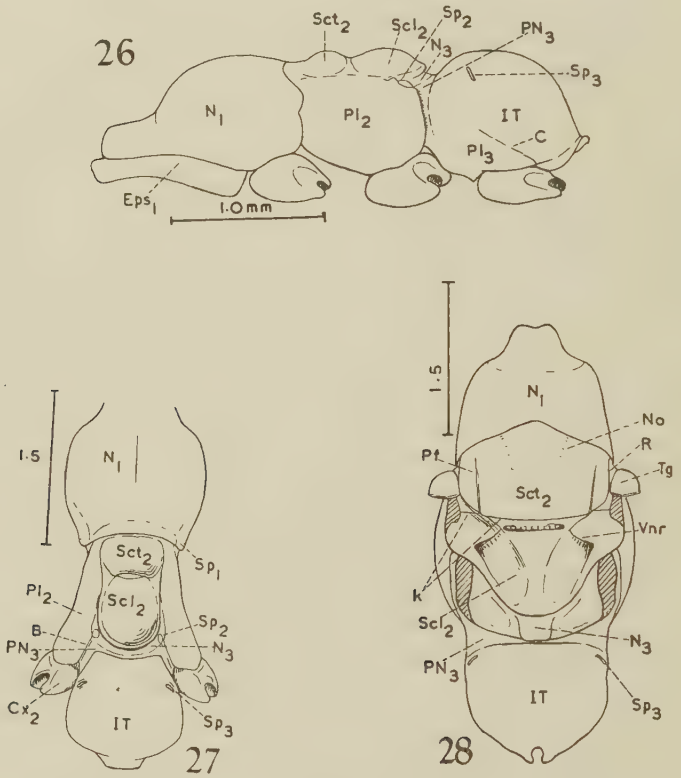
thorax of *Bradynoboenus gayi* Spin., while fig. 25 shows the lateral aspect of the male. The thorax of the female falls into the same class as that of *Myrmosa*, having the pronotum free and the rest of the thorax fused together. It approaches most closely in structure to the female thorax of *Apterogyna* and as is shown later the two genera have other characters in common. There is a single incomplete suture on the dorsum which may be homologous with the similar one in *Apterogyna*, but in *B. gayi* it looks more like the suture between the metanotum and propodeum than that between the mesonotum and metanotum plus propodeum; it is set with long erect bristles. Immediately posterior to this suture is the propodeal spiracle, and antero-lateral to the spiracle is a short line touching it which may possibly be a portion of the meta-pleural-propodeal suture. The meso-metapleural suture is well marked and dorsally meets a longitudinal groove which is probably the suture between the pleura and the dorsum; what I take to be the metathoracic spiracle does not, however, lie at the point of junction of these two sutures as is normally the case, but is on the meso-metapleural suture ventral to the presumed dorso-pleural suture. Either the longitudinal suture is secondary and is not that separating the dorsum from the pleura, which is unlikely, or the metathoracic spiracle is not in its normal position, as occasionally happens (Tulloch, 1935, female of *Dorylus helvolus* (L.)). Anterior to the meso-metapleural suture is a well-marked line of outstanding bristles, indicated by a dotted line in the fig. (24); the line commences dorsally at the metathoracic spiracle and terminates ventrally before the second coxa; it may possibly indicate a prepectus, but if this is so the prepectus dorsally occupies the full length of the mesopleuron. In the female thorax of *B. gayi*, as the figures show, there has been considerable alteration in the shape and relative sizes of the parts of the thorax, other than the mesothorax, compared with the male. In particular the pronotum has become relatively very much larger; in the male the huge mesonotum has reduced the pronotum antero-medially to a vertical collar, while in the female this part of the pronotum has been extended posteriorly until it is almost level with the postero-dorsal angles. This type of change in the pronotum which has not been mentioned hitherto, except in *Typhoctes*, will be frequently met with later on. The thorax of the male of *B. gayi* is thickly covered with rufous hairs, beneath which the sclerites are black and punctured; the female thorax is glabrous except for the lines of bristles, and is testaceous and impunctate. The legs of the female are more powerful than those of the male and are much like those of female Tiphiidae.

Material examined :—*Bradynoboenus gayi* Spin. male and female, *B. wagenknechti* Reed, male.

7. Thynnidae (Methocinae).

Figs. 27 and 26 are dorsal and lateral views of the female thorax of *Methoca ichneumonides* Latr., and fig. 28 shows the dorsal aspect of the male. In the female, although the thorax is greatly modified compared with that of the male, there has been little or no fusion of the parts of the dorsum and all of them can be easily identified. The pronotum is relatively larger than that of the male and is somewhat globose and is freely articulated with the meso-thorax; the increased size is probably connected with the larger forelegs of the female. The scutum and scutellum of the mesonotum form a pair of rounded and convex areas of which the scutellum is somewhat the larger; both are very much narrower than those of the male and in consequence the prominent mesopleura are completely visible from above, projecting on either side of the

mesonotum. The metathoracic spiracle is large and is guarded by a small circular sclerite, much like that of many worker ants. The metanotum is a sunken area slightly overhung by the posterior border of the scutellum. Between the metanotum and the propodeum is the very narrow metapostnotum. The propodeum is globose and inclusive of the metapleuron is about the same size as the pronotum. Laterally the meso-metapleural suture is as well defined as that of the male. The metapleural-propodeal suture is almost obliterated. There is a section of the Methocinae in which the mesoscutum of the female thorax is not convex as in *M. ichneumonides*, but is flat or a little depressed



Figs. 26–28.—*Methoca ichneumonides* (Thynnidae), 26, ♀, lateral; 27, ♀, dorsal; 28, ♂, dorsal.

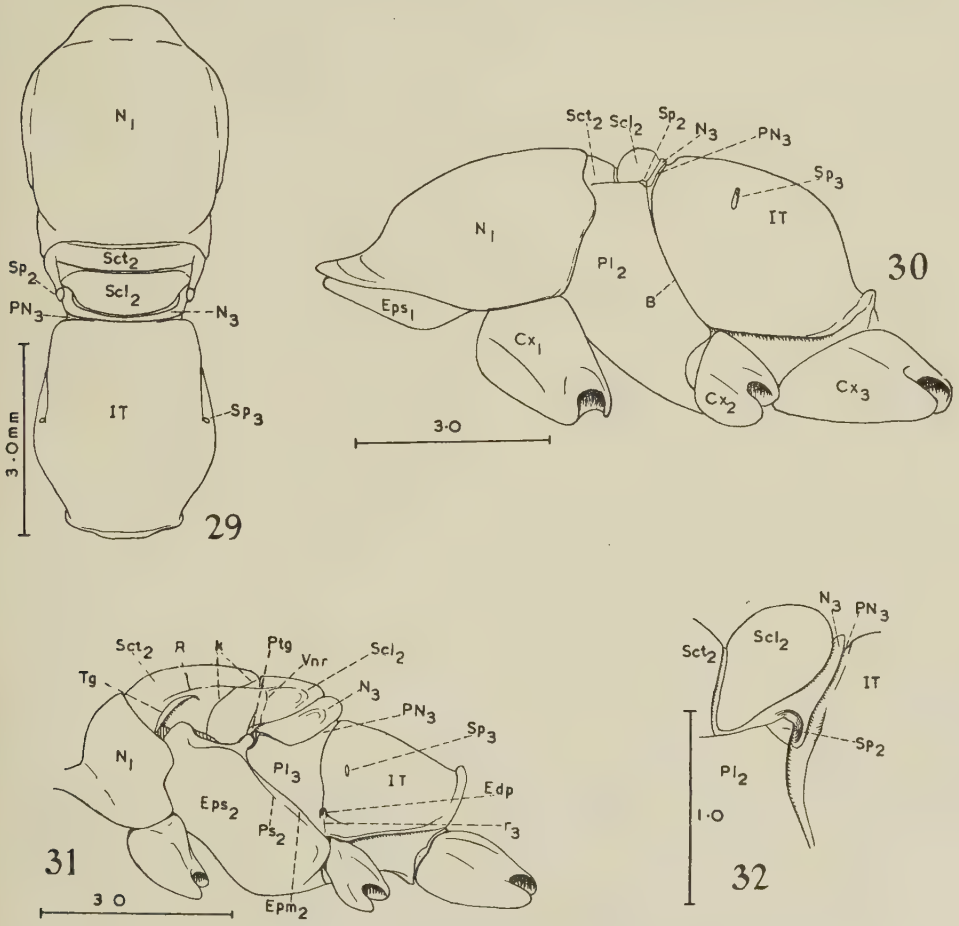
(Williams, 1919); *M. punctata* Wllms., which I have seen, is such a species. In these forms the anterior part of the mesothorax tends to become petiolate, and is often longitudinally striate.

Material examined:—*M. punctata* Wllms., *stygia* Say, *smithii* Magr., *bicolor* Cam., *haemorrhoidalis* Westw., *minima* André.

8. Thynnidae (Diamminae).

There is only one species in this subfamily of the Thynnidae, *Diamma bicolor* Westw., confined to Australia. Figs. 29 and 30 show dorsal and lateral views of the thorax of the female and fig. 31 a lateral view of the male. The

female thorax is of the same type as that of *Methoca ichneumonides* Latr., but the modifications have been carried somewhat further; the whole insect is rather similar in appearance to a female *Methoca*. The mesonotum is considerably shorter than that of *Methoca* and the disparity in size between the scutum and scutellum is more pronounced; the former is considerably shorter than the latter and is flat, while the scutellum is convex; the two areas are separated by a deep groove which expands laterally to form what are probably

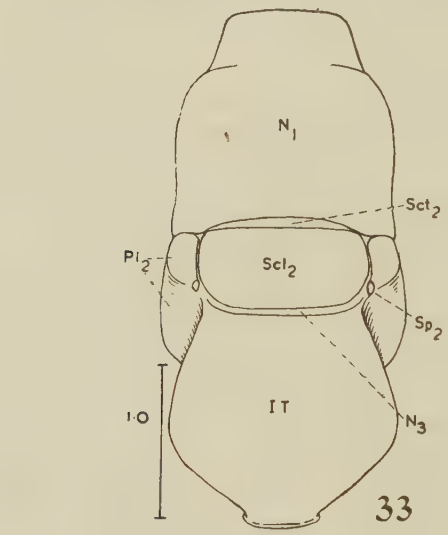


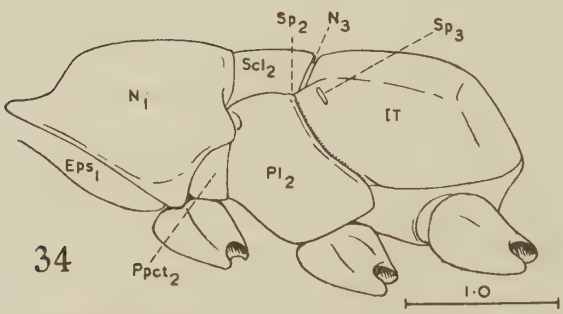
FIGS. 29–32.—*Diamma bicolor* (THYNNIDAE), 29, ♀, dorsal; 30, ♀, lateral; 31, ♂, lateral; 32, ♀, lateral view, large scale, of the area around the second spiracle.

the notal axillae, the groove being composed of part of the axilla and the transcutal suture. As in *Methoca* the metapostnotum and metanotum are visible; fig. 32 shows an enlarged lateral view of this part of the thorax. The meso-metapleural suture is well marked while the metapleural-propodeal is obliterated; the endophragmal pit lies on or close against the meso-metapleural suture. The position of the propodeal spiracle in the female, compared with the position in the male, indicates that the anterior region of the propodeum in the female has become relatively longer.

9. Thynnidae (Rhagigasterinae).

Figs. 33 and 34 show the dorsal and lateral aspects of the female thorax of *Rhagigaster ephippiger* (Guér.). The thorax is of the same type as that of *Diamma bicolor* Westw., but is rather more modified. While the dorsum of the female of *Methoca ichneumonides* Latr. consists of a series of convex surfaces, that of *Rhagigaster ephippiger* is much flattened and forms a surface almost in one plane, interrupted by sutures. The female thorax of *Diamma bicolor* is





Figs. 33–34.—*Rhagigaster ephippiger* (Thynnidae), 33, ♀, dorsal; 34, ♀, lateral.

somewhat intermediate in this respect between those of *Methoca* and *Rhagigaster*. In *R. ephippiger* the scutum is now reduced to a small transverse area, and the mesonotum consists almost entirely of the scutellum, while the suture between the two is much less pronounced than that of *Diamma*; probably the scutum is not quite as small as it appears, for it is to some extent covered by the posterior margin of the pronotum which is a little produced posteriorly. The metanotum is deeply sunk between the scutellum and propodeum, and the metapostnotum is no longer separately visible. Laterally there is a curious prepectal sclerite which is only connected by membrane to the mesopleuron; the ventral or sternal portion of this prepectus is not developed or has become

desclerotised so that the prepectus consists of two very freely articulated lateral sclerites. Normally these prepectal sclerites are hidden beneath the pronotum but, as in the example figured, the specimen may be pinned in such a way as to reveal them; they are present also in *Methoca* and *Diamma*. For further discussion of this prepectus see pages 400, 401 and 403. The mesopleuron is abruptly prominent and has a well-marked dorsal surface (fig. 33) contiguous with the scutellum. Turner (1910) makes use of this character to separate the females of the RHAGIGASTERINAE from those of the THYNNINAE which lack this dorsal mesopleural surface. The epimeron of the mesopleuron which is visible in the male is also faintly marked in the female. The meso-metapleural suture is well developed while the metapleural-propodeal suture is obliterated. The propodeum is markedly angular, for it is wider dorsally than ventrally and the dorsal and lateral surfaces meet abruptly. The propodeal spiracle is much

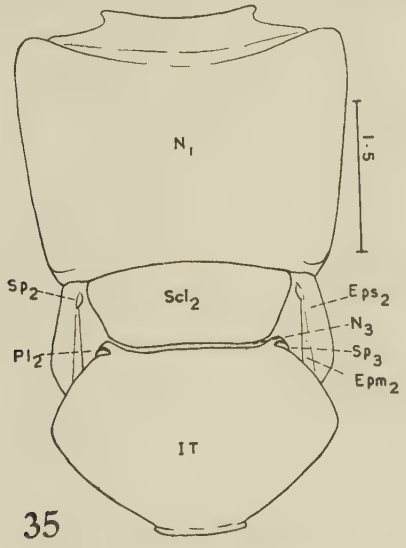


FIG. 35.—*Thynnus ventralis* (THYNNIDAE), ♀, dorsal.

more anterior in position than in *Methoca* or *Diamma*, but it occupies this anterior position in the male, the thorax of which is generally similar to that of the male of *Diamma bicolor*.

10. THYNNIDAE (THYNNINAE).

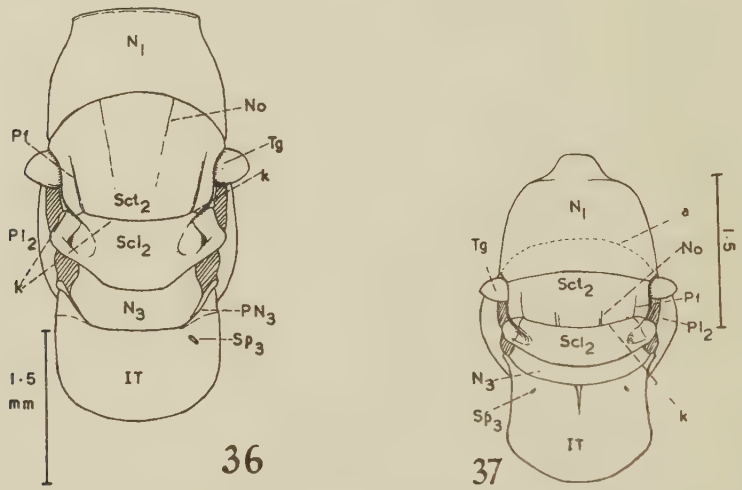
Fig. 35 is a dorsal view of the female thorax of *Thynnus ventralis* Sm. It is essentially similar to that of the female of *Rhagigaster ephippiger* but differs in matters of detail of which the following are the more important. The mesoscutum is more reduced and is hidden beneath the posterior edge of the pronotum which is closely applied to it. The propodeum has become more angular and the dorsal surface overhangs the lateral surfaces more strongly. The mesopleuron, though abruptly prominent, lacks the dorsal surface as already explained.

Material examined in the RHAGIGASTERINAE and THYNNINAE:—*Rhytidogaster* spp., *Scotaena* spp., *Hemithynnus australis* (Gray), *T. mutandus* Turn., etc.

The female thorax of the Thynnidae exhibits in a number of respects a progressive increase in specialisation (see also p. 417) as one passes from the Methocinae to the Thynninae. There is a progressive increase in the angularity of the pronotum and propodeum, commencing with the globose condition of *Methoca* and reaching a maximum degree of angularity in such forms as *Thynnus ventralis* just described; in step with this is a progressive flattening of the dorsum, the simplification and modification of the mesonotum (in particular the increase in size of the scutellum and the corresponding reduction of the scutum), and the fusing of the metanotum and metapostnotum into a simple groove between the scutellum and propodeum.

11. Tiphiidae.

Unlike the families dealt with so far, the females of most of the species in this family are winged and only a few are flightless, but the thorax always

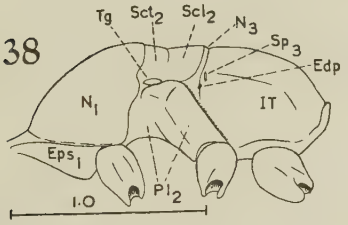


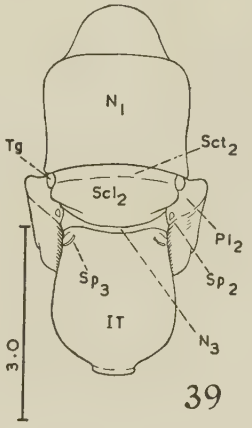
Figs. 36–37.—*Meria tripunctata* (Tiphiidae), 36, ♂, dorsal; 37, ♀, dorsal.

displays sexual dimorphism. In those females which are entirely apterous, the thorax is strikingly like that of the Rhagigasterine Thynnids; from this extreme condition there is a continuous series leading back to species in which the female is fully winged. But even in species with fully winged females the thorax, as indicated above, is distinctly different from that of the male and is plainly tending towards the condition of the entirely apterous forms. Figs. 36 and 37 are dorsal views of the thorax of the male and female of *Meria tripunctata* (Rossi), and they serve to show some of the differences that exist between the thoraces of the males and females in this family, for the female of this species is fully winged. The pronotum of the female is longer than that of the male and is of a different shape; it is produced posteriorly so that it apparently conceals the anterior portion of the scutum which can be seen through it. The meso- and metanota taken together are relatively shorter than those of the male; expressing this numerically, the length of these two sclerites in a female, measured from the anterior edge of the mesonotum seen through

the pronotum, to the posterior edge of the metanotum along the median dorsal line, relative to the total length of the thorax, was as 1 : 2·1. The same lengths in a male were as 1 : 1·8. The mesopleura of the female are more prominent than those of the male. If the thorax is looked at in side view it is seen that the mesonotum of the female is depressed compared with that of the male. The inference is that the decrease in size of the mesonotum in the female reflects weaker powers of flight than those of the male, and that the increase in size of the pronotum and in the prominence of the mesopleura is correlated with the more powerful legs of the females which are highly adapted for digging.

The majority of the short-winged and wingless forms occur among the MERIINAE in which sexual dimorphism is always very marked; in the TIPHIINAE, where the sexes are not so different, I have seen only one short-winged species, *Tiphia brevipennis* Lucas. However, in the TIPHIINAE there are the same differences between the thoraces of the males and females as





FIGS. 38–39.—38, *Braunsomeria atriceps* (TIPHIIDAE), ♀, lateral; 39, *B. mutilloides*, ♀, dorsal.

described in the MERIINAE. In the SCOLIIDAE *sensu stricto* (*Scolia* etc.) I have not seen any marked sexual dimorphism in the thorax.

Turning to the apterous forms, fig. 38 is a lateral view of the female thorax of *Braunsomeria atriceps* Turn., while fig. 39 shows the dorsal aspect of *B. mutilloides* Turn. ♀. The similarity between the thorax of these forms and those of female Thynnids is at once apparent and it will only be necessary to describe the minor points in which they differ. The scutum of *B. atriceps* is not greatly reduced, but this is probably due to the condition of aptery being incomplete, for the tegulae are still well developed. The most important difference, and it applies to *B. mutilloides* and other species as well, is that the metanotum is at the same level as scutellum and propodeum, instead of being deeply depressed between them as in the majority of the THYNNIDAE. As can be seen in the figure of *B. mutilloides*, the mesopleura have a well-developed dorsal surface as in the Rhagigasterine Thynnids. In *B. mutilloides* modification of the thorax has proceeded farther than in *B. atriceps*; the tegulae are very small and the scutum is considerably reduced and only weakly divided from the scutellum, while the mesopleura project very strongly; they project anteriorly as well as

laterally so that a re-entrant angle is formed between each projecting part and the remainder of the mesopleuron that lies between the postero-lateral margin of the pronotum and the base of the projection.

Material examined :—*Tiphia femorata* Fab., *implicata* Cam., *tibetana* Turn., *beckeri* Tourn., *Iswara tartara* (Sauss.), *Pseudomeria dakarensis* Buyss., *perornata* Turn., *Braunsomeria arnoldi* Turn., *albohirta* Turn., *quadraticeps* Turn.

12. Possible affinities of the groups of Scolioid wasps dealt with in the previous pages.

In all the groups comprising this section, except the Tiphiidae (*Tiphia*, *Meria*, etc.), the females are always wingless. The relationships of the family and other units that make up this Scolioid group of wasps are not at all clear, and until some of the more serious gaps in our knowledge of them are filled in, it is unlikely that anyone will be able to suggest a very satisfactory scheme of classification or affinity. As Saussure (1892) has remarked, many of the characters which at first seem likely to prove of value in classification are found on closer examination to be shared by groups that are obviously not closely allied, as well as by those that are. In *Typhoctes* Ashm., and *Brachycistis* Fox, it seems that only one sex is known, and in the majority of the groups nothing, or exceedingly little, is known of the habits.

In discussing the possible affinities of the groups, I propose to arrange them according to the condition of the thorax in the wingless females, and then to see how various other characters agree with this arrangement.

Class I. The dorsum of the thorax in the female fused into one piece, with no functional sutures :—Mutillidae *sensu stricto*.

Class II. The dorsum of the thorax divided into two parts by a functional suture between the pronotum and the remainder of the thorax, which is composed of the meso- and metanota and propodeum fused together :—*Myrmosa*, *Apterogyna*, *Chyphotes*, *Bradynoboenus*.

Class III. The dorsum of the thorax divided into three primary parts, the pronotum, the meso- and metanota, and the propodeum :—*Typhoctes*, Thynnidae, Tiphiidae.

This arrangement suggests that the Mutillidae occupy an isolated position, and this is borne out by the evidence of other characters. The males have several characters that serve to distinguish them from the other groups. For example, the hind-wings lack an anal lobe, and the condition of the metapleuron is distinctive (fig. 2), for the suture between it and the propodeum is well developed and the pleuron is sharply divided into dorsal and ventral parts by an approximately horizontal suture. This character of the condition of the metapleuron may be an important one, for as far as my observations go they show that within each of the groups under consideration the condition of the metapleuron is very constant, excepting for slight differences in the degree of development of the metapleural-propodeal suture.

In general the male genitalia of the Mutillidae are very characteristic of the family, but it is not possible to define categorically the characters which distinguish them from the other groups, because there are too many exceptions to the type characteristic of the family. Broadly speaking, this conclusion is in agreement with the conclusions of Richards (1934) and Peck (1937). The most that one can do here is to draw attention to the distinctive features of the

type of genitalia that is most representative of the family as a whole; in doing so I make use of the nomenclature proposed by Peck (1937 : 223–224). In the most typical Mutillid genitalia the gonoforceps are long, tapering and cylindrical and often somewhat divergent; frequently they project from the end of the abdomen, forming the pair of spines used as a character to distinguish the males of this family. Dorsally the gonostipes form a pair of prolongations medial to the gonoforceps; the two lobes of the volseliae are well developed; the aedeagus is shorter than the volsellae and both are much shorter than the gonoforceps. For figures of the male genitalia of MUTILLIDAE see Radoszkowski (1885) and Mickel (1928).

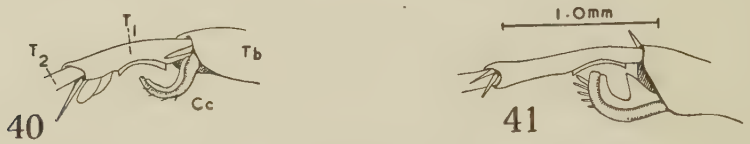
Of all the characters that seem to indicate that the MUTILLIDAE are somewhat isolated, the most important single character seems to be that of the female thorax, which in its highly developed secondary condition is sharply distinct from that of any of the other groups. The group with which the MUTILLIDAE seem to have the most affinity through characters common to both, is that containing *Myrmosa*, which though itself rather isolated, is perhaps a connecting link between the MUTILLIDAE and the other members of class II. It is the general rule that the females of *Myrmosa* and the MUTILLIDAE have the mesopleura flat or concave, whereas in the other groups they are always projecting, usually strongly so. This condition of the mesopleura probably reflects the degree of development of the coxal and other muscles of the intermediate pair of legs, and the degree of development of these and the other legs may be in turn an indication of the habits of the insects. Certainly it is a fact that the female Tiphiids and Thynnids, which commonly burrow in the ground in search of the beetle larvae that form their usual prey, have the legs very powerfully developed; while the females of *Myrmosa* and the MUTILLIDAE, where the legs are not noticeably more powerful than those of the males, are probably often able to enter the preformed burrow of some other aculeate in order to oviposit. The males of *Myrmosa* and the MUTILLIDAE lack the upturned aculeus upon the eighth sternum which is present in the other males of class II. Both males and females of *Myrmosa* and the MUTILLIDAE have the intermediate coxae contiguous and lack any scales or projections on the posterior border of the second sternum, whereas in the other groups if the coxae are close together then the sternum has scales, or if scales are absent the coxae are well separated.

As already remarked, *Myrmosa* seems to occupy a rather isolated position in class II; it is not that it has very striking peculiarities which serve to distinguish it from the rest of class II, but rather that it lacks so many of the characters occurring in the other members of this class. The following characters are peculiar to *Myrmosa*. The shape of the eighth sternum in the male (Malloch 1926, fig. 2) which appears to be much the same throughout the genus; it is somewhat spoon-shaped and only the tip of the middle lobe projects beyond the other sterna. The abdominal segments of the male are each constricted near the base, a condition not seen in any of the other members of this group, nor in the MUTILLIDAE, but the general rule in the males of the THYNNIDAE and the MERIINAE. The posterior coxae in both sexes are developed dorsally into a leaf-like expansion. Mr. Paul Freeman has kindly allowed me to quote from an unpublished paper of his on the wing-coupling apparatus of the Hymenoptera Clistogastra. He divides the hamuli of the hind-wings into two groups, the distal and sub-basal, of which the latter seem to be the most valuable taxonomically. Examination of these sub-basal hamuli in the members of class II and the MUTILLIDAE shows that the males of *Myrmosa* have a few short ones, but the male MUTILLIDAE and the other

members of class II lack any sub-basal hamuli, while they are present in class III. The venation of the fore-wings of *Myrmosa* is complete and the females have ocelli, but in the rest of class II the venation stops short of the end of the wings and the females lack ocelli. The one obvious character that seems to connect *Myrmosa* with the rest of class II is the important one of the bipartite condition of the female thorax.

Passing now to a consideration of the other members of class II—*Apterogyna*, *Chyphotes* and *Bradynoboenus*—*Apterogyna* has often been placed in the MUTILLIDAE and is placed there by Bischoff (1920) in his monograph of the African MUTILLIDAE, but it certainly does not belong there. It is a very distinct genus, particularly on account of the nodiform first abdominal segment, the constriction between the second and third segments, the reduced venation, the male genitalia, and the tibial spurs and other characters. *Apterogyna* certainly merits a separate family or subfamily, but there is a number of characters which it shares with *Chyphotes* and *Bradynoboenus*.

Apterogyna and *Chyphotes* have on each side of the second abdominal tergite a longitudinal stripe of hairs; this is a common feature in the MUTILLIDAE where it is called a felt line. The females of *Apterogyna* lack the hairs but have a well-defined groove or slit opening upwards. Presumably the structure is the opening of some kind of a gland, and the hairs, when present, have to do



FIGS. 40–41.—Calcaria of fore tibia of, 40, *Bradynoboenus gayi* ♂; 41, *Apterogyna savignyi* ♂.

with the retention or dissemination of the secretion. The character that is most suggestive of a connection between *Apterogyna* and *Chyphotes* is the shape of the female thorax (figs. 17, 18, 21, 22); except that the hind part of the thorax of *Chyphotes* is rather more globular and has lost all traces of sutures, it is very like that of *Apterogyna*. The males of both genera have an upturned aculeus on the eighth sternum.

Two characters may be mentioned to show that a connection exists between *Apterogyna* and *Bradynoboenus*. The first is a curious similarity in the nature of the tibial spurs (figs. 40 and 41). In both genera the spur of the front tibia is stout and sickle-shaped and quite unlike the corresponding structure in the majority of these Scolioid wasps. The spurs of the mid and hind tibiae of *Apterogyna* are most distinctive, being large, ivory white and very coarsely pectinate; those of *Bradynoboenus*, though of a normal ferruginous colour, are slightly pectinate and apparently of the same type as those of *Apterogyna*. The second character is that of the venation; in both genera the venation is very reduced and in the fore-wings is confined to the basal third of the wing. The venation of *Bradynoboenus* is rather more reduced than that of *Apterogyna*. The intermediate coxae of *Chyphotes*, *Apterogyna* and *Bradynoboenus* are widely separated but there are no projections, scale-like or otherwise, on the second sternum.

As regards the peculiarities of *Chyphotes*, the metapleuron of the males is distinctive (fig. 19), for the endophragmal pit is very close to the meso-meta-

pleural suture, and ventral to this pit the metapleuron appears to become so narrow as to be linear. What appears to have happened is that the portion of the metapleural-propodeal suture ventral to the endophragmal pit has become obliterated as often happens, and thus the secondary suture which runs ventrally from the pit and becomes contiguous with the meso-metapleural suture, at first sight appears to be the true metapleural-propodeal suture in an unusual position. This secondary suture may possibly be that dividing the metapleuron into dorsal and ventral portions, which has become very oblique. This suggested explanation of the condition of the metapleuron in *Chyphotes* is supported by a consideration of the thorax in such forms as *Rhopalosoma guianense* Schulz, *Hadropompilus montanus* Arn. (fig. 57) and *Diamma bicolor* Westw. (fig. 31).

The position of *Brachycistis* is very uncertain, chiefly because the females are apparently unknown. Like *Chyphotes*, to which it is usually considered to be most closely allied, it is confined to North America. It bears a strong resemblance to *Chyphotes*, but the two genera have few striking characters in common. Malloch (1926) considers *Brachycistis* to be more closely allied to the TIPHIIDAE than to any other group, and in this he may be correct. One of the most important characters that supports this view is the presence of a well-developed pair of scales on the second sternum, which project between the bases of the second pair of coxae. This character is very typical of the TIPHIIDAE and the other groups in class III but is not present in the members of class II. On the other hand, *Brachycistis* lacks the peculiar prepectal sclerites which seem to be characteristic of the members of class III. The venation of *Brachycistis* is more like that of *Chyphotes* than that of *Tiphia* and the same applies to the male genitalia, except that according to Malloch the cerci (pygopods of Peck, 1937) are much reduced or absent in which they agree with the condition in the TIPHIIDAE, but one might mention that these structures are also absent in *Apterogyna* (Radoszkowski, 1885; Saunders, 1899). At first sight one is struck by the similar appearance of the eyes and ocelli in *Brachycistis* and *Chyphotes*. The eyes are very prominent and the ocelli of great size, but it is probable that this is a case of parallelism due to adaptation to nocturnal habits; one sees much the same thing in certain species of *Apterogyna* and in some genera of MUTILLIDAE such as *Photopsis*.

It is very unlikely that Malloch is correct in supposing that *Typhoctes peculiaris* (Cress.) is a female of some species of *Brachycistis*, for there are important differences which he himself admits. Both *T. peculiaris* and *T. guatemalensis* Turn. have a felt line on each side of the second abdominal tergum, and as far as I am aware this structure when present always occurs in both sexes and is commonly more strongly developed in the male; *Brachycistis* has no felt line, it has scales on the second sternum and the intermediate coxae are subcontiguous, while *T. peculiaris* lacks any scales on the second sternum and the intermediate coxae are wide apart; as the single specimen of *T. guatemalensis* is gummed on a card I have not been able to examine the sterna. As far as my observations go, sternal scales, when present, always occur in both sexes and the coxae are about the same distance apart. *T. peculiaris* and *guatemalensis* have two spurs on each middle tibia but *Brachycistis* is exceptional in having only one. The character mentioned by Malloch of the suture between the meso- and metapleura being oblique in *Brachycistis* and *T. peculiaris* is of little value because the apterous thorax of *Typhoctes* is much modified, and on account of the reduction of the mesonotum this suture undoubtedly occupies a secondary position. If Malloch is correct in supposing that *Brachycistis* is

allied to the TIPHIIDAE, then one would expect that the females, if wingless, would display a condition of the thorax similar to that of the wingless MERIINAE such as *Braunsomeria* spp. (figs. 38 and 39) and the female Thynnids. The most characteristic feature of the thoraces of these forms is the abruptly projecting mesopleura; the thorax of *Typhoctes guatemalensis* Turn. does not possess this feature and bears no particular resemblance to the thoraces of these forms except that it is tripartite.

If one accepts the view of Bradley (1917) that the females provisionally associated with *Brachycistis* by Fox under the names *B. rutilans* (Blake), and *B. bimaculata* Fox, do not really belong here, but are more probably related to *Myrmosa*, then the true females of *Brachycistis* are unknown. Until the females of this genus are known its real affinities must remain a problem; if it belongs with the members of class III, then the females, if wingless, should have a tripartite thorax; if with class II then a bipartite thorax.

Most of the characters of the females of *Typhoctes* have been discussed in dealing with *Brachycistis* so that it will be as well to consider the position of this genus now, rather than when dealing with the rest of class III. It is very doubtful if the males are known; those under the name *T. attenuatus* (Blake) are put in the genus only on surmise. Although the thorax of *T. guatemalensis*, and presumably that of *T. peculiaris* also, is tripartite, the balance of evidence seems to place these forms in class II rather than class III; for example, *T. peculiaris* lacks the scales on the second sternum typical of class III, and both species have a felt line, which, excepting for the MUTILLIDAE, does not occur outside class II.

It will be convenient to discuss the position of *Bradynoboenus* now, for it has a number of points of resemblance with the members of class III, which are considered next. It has been shown that *Bradynoboenus* has connections with *Apterogyna*, and one may add here that the somewhat rounded outline of the female thorax, when viewed from above, shows some similarity to those of *Apterogyna* and *Chyphotes*. A further point is that so far as I can make out from the specimens I have examined, *Bradynoboenus* lacks the prepectal sclerites seen in the members of class III. On the other hand, the following characters suggest affinities with the members of class III. The male has a three-spined eighth sternum suggestive of the condition in many male Thynnids. The shape of the head in the female is like that of the females of the MERIINAE, though it lacks ocelli which the latter possess. The tufts of hairs on the antennal scapes, and the tufts and lines of hairs on other parts of the body, parallel the condition in the wingless females of *Braunsomeria*. The powerful legs of the females are closely similar to those of the male of the TIPHIIDAE and THYNNIDAE. Saussure (1892) pointed out the resemblances between *Bradynoboenus* and *Meria* (in the sense of Saussure). Zavattari (1910) is impressed by these resemblances and strongly criticised Ashmead's placing of *Bradynoboenus* in his family MYRMOSIDAE (1903); but in criticising this placing of *Bradynoboenus*, Zavattari only takes into account the single character of the bipartite female thorax used by Ashmead. But the other characters that connect *Bradynoboenus* with *Apterogyna* and *Chyphotes* show that it is intermediate in many respects between class II and class III, while possessing several characters peculiar to itself. Of these peculiar characters one may mention the enormous mesonotum of the male which overhangs the pronotum anteriorly and the propodeum posteriorly; also the reduced maxillary and labial palpi, of which the former (Blake, 1886) are 3-segmented and the latter 2-segmented. It seems, then, to be a matter of choice whether one follows Ashmead in allying

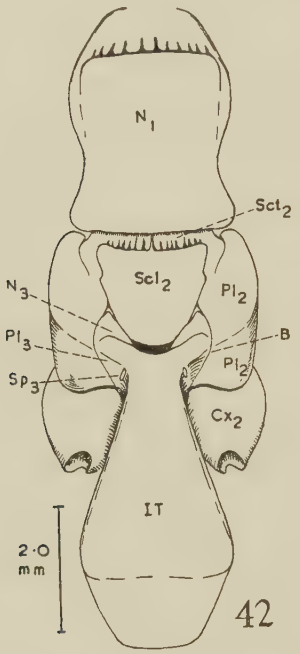
Bradynoboenus with the other members of class II, or agrees with Zavattari's suggestion that it should be placed as a separate subfamily of the SCOLIIDAE. There can be little doubt that its nearest allies among class III are such genera as *Pseudomeria* and *Braunsomeria*; the similarity in appearance of the females coupled with the strong tendency of the females of the latter genera to become wingless support this idea. I prefer to place *Bradynoboenus* in class II, for the bipartite female thorax, the lack of scales on the mesosternum, and the lack of free prepectal sclerites appear to me to be strongly in favour of this course.

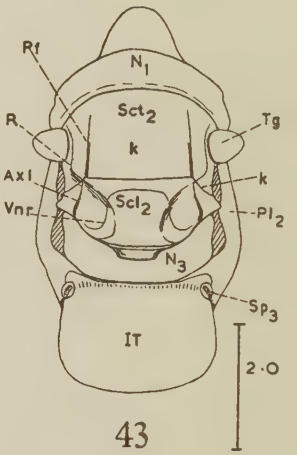
Turning now to the members of class III minus *Typhoctes*; the grouping together of the THYNNIDAE, including *Methoca*, and TIPHIIDAE is in accordance with the usual classification of these groups and one can therefore deal more briefly with the evidence. So far as their habits are known, these insects are all parasitic upon beetle larvae. The thorax of the short-winged and wingless females among the TIPHIIDAE bears a close and detailed resemblance to the thorax of the female Thynnids of the subfamily RHAGIGASTERINAE. The thorax of the female of *Diamma bicolor* Westw. (THYNNIDAE, DIAMMINAE) is intermediate in condition between the thoracic type of the rest of the THYNNIDAE and that displayed by *Methoca*. The male genitalia of *Diamma bicolor* and *Methoca ichneumonides* Latr. bear a considerable resemblance to one another. All possess scale-like processes on the posterior border of the mesosternum, which project over or between the bases of the second pair of coxae; though in *Methoca* these are hardly more than a pair of tooth-like structures. So far as I have been able to see, all possess the rather peculiar prepectal sclerites described in *Rhagigaster ephippiger* (Guér.), the chief features of which are their high degree of separation from the mesopleura, their concealment beneath the pronotum and the lack of any sclerotised sternal region connecting them.

The foregoing discussion of the apparent relationships of these groups of Scolioid wasps in which wingless females occur, shows that in the main Ashmead's grouping of these families (1900–4) is a natural one. He places *Methoca* as a subfamily METHOCINAE in the THYNNIDAE, but Turner (1910) excludes this genus from the THYNNIDAE. However, *Diamma* so clearly connects *Methoca* with the main body of the THYNNIDAE that it seems best to include it in this family. Ashmead's table to the families of the Vespoidea requires correction so far as his family MYRMOSIDAE is concerned, for the middle coxae of most of the groups in the family are widely separated and not contiguous; the same applies to the THYNNIDAE. He considered the THYNNIDAE to be most closely allied to the MYRMOSIDAE and MUTILLIDAE, but it may be seen that in fact they belong with the TIPHIIDAE. If instead of the character of the middle coxae being widely separated or contiguous, one substitutes that of the presence or absence of scales on the posterior border of the mesosternum, I think these errors are corrected and the THYNNIDAE take their proper place in the key next to the TIPHIIDAE and SCOLIIDAE. This change would also move *Brachycistis* to the neighbourhood of the TIPHIIDAE, which may not be correct.

The problem of what status to assign to the groups that Ashmead placed in his family MYRMOSIDAE (class II in the foregoing pages) is a difficult one. As may be seen, they are so distinct from one another that by analogy with the other families they should each be raised to family rank; but on the other hand so little is known of them and they are mostly so small, *e.g.*, *Bradynoboenus* with only about 2 species, that it is convenient to treat them as subfamilies of a single family MYRMOSIDAE. An alternative scheme that would have the advantage of emphasising the difference between classes II and III, the members of which have frequently been associated together in various incorrect

ways in the past, would be to call class III the Scoliiformes and class II the Myrmosaeformes, or to merge the MUTILLIDAE with class II under such a name as Mutilliformes, and to treat the various groups within it as separate families as their degree of structural divergence warrants. Probably the SCOLIIDAE proper and perhaps the FEDTSCHENKIIDAE and ANTHOBOSCIDAE would go into the Scoliiformes. These two groups, the Scoliiformes and Mutilliformes, would then form convenient, and I think natural, subdivisions of a superfamily such as the Heterogyna (Wheeler, 1928) or Scolioidea.





FIGS. 42–43.—42, *Mangesia incerta* (BETHYLIDAE), ♀, dorsal; 43, *M. atopogamia*, ♂, dorsal.

13. Bethyloidea.

This superfamily is considered next, as the BETHYLIDAE themselves are so clearly related to the Scoliiformes. In view of the very considerable structural differences within this group, it seems more correct to treat them as families than as subfamilies of the BETHYLIDAE.

(i) BETHYLIDAE.

In this family the thorax of the wingless forms seems to be of two types. The type to which the majority belong is very like that of the wingless Scoliiformes. The second type is seen in such genera as *Mesitius* which connect the BETHYLIDAE with the CHRYSIDIDAE and CLEPTIDAE. *Mangesia incerta* Turn. will serve as a convenient example of the first type on account of its large size. The thorax of the female of this species (fig. 42) is a very strange one, and at first some of the details of structure are difficult to interpret; but despite these minor peculiarities, it has a very strong resemblance to the thorax of the more

highly modified forms among the Scoliiformes, in particular to such forms as *Braunsomeria mutilloides* (fig. 39); all the most characteristic features of the thorax of the latter are present in the thorax of *Mangesia incerta*. The dorsum is much flattened, the pronotum is much larger than in the male (fig. 43), it is oblong and its posterior dorsal margin is produced some way over the scutum, which is reduced to a transverse area much smaller than the scutellum. The propodeum is wider above than below and the dorsal and lateral surfaces meet at a sharp angle; the propodeal spiracle is close to the anterior margin of the propodeum. The mesopleura project very abruptly on either side and have a well-marked dorsal surface in about the same plane as the scutellum; anteriorly each mesopleuron projects so abruptly that a re-entrant angle is formed between the projection and the side of the thorax.

Turning now to the features peculiar to *Mangesia incerta*, the postero-ventral angles of the pronotum nearly meet in the mid-ventral line, where they overlie the well-developed prepectus; the latter is divided from the mesothorax which overlaps it, but unlike the condition in the Scoliiformes the sternal portion is present, though there is a complete suture in the mid-ventral line. Probably the Scoliiforme type of prepectus was derived from the normal type via such a condition as is seen here. Widening of the median ventral suture would lead eventually to desclerotisation of the sternal portion, and this, in conjunction with an increase in the tendency to separation from the mesothorax and concealment beneath the pronotum, would lead to the condition found in the Scoliiformes. The scutum is a deep crenate groove, partially concealed beneath the pronotum. Laterally and posteriorly the scutellum has a projecting downturned rim, beneath which is a deep groove in which the second spiracle is probably concealed, for laterally the groove appears to separate the mesopleuron and scutellum. There is a deep pit in the median dorsal line between the propodeum and scutellum; the floor of this pit appears to be formed by the metanotum which has here been invaginated; a similar though less exaggerated condition is seen in the male (fig. 43, *M. atopogamia* Turn.). On either side of this pit a part of the metanotum is visible and touches the scutellum. The propodeum is very long and narrows anteriorly, forming a waist at about the level of the propodeal spiracles beyond which it expands again.

In all but minor details the thoraces of the wingless females of *Pristocera*, *Pseudisobrachium* and *Apenesia* are the same as that of *Mangesia incerta*. The chief difference to note is that in some of the species the mesoscutum is not depressed and may be so fused with the scutellum that it is difficult to see the line of junction. The median dorsal pit between the scutellum and propodeum is most often missing and it seems possible that the whole of the metanotum has been invaginated until the posterior border of the scutellum meets the anterior border of the propodeum; the appearance of this part of the thorax (see fig. 44 of *Scleroderma domesticum* Latr.) suggests this idea. The other and more normal explanation is that the metanotum has become indistinguishably fused with the propodeum. The figures of the thorax of *Cephalonomia quadridentata* Duch. given by van Emden (1931) favour the second explanation. His figures were drawn from specimens mounted on slides in which an invagination of the metanotum would be plainly visible; but the lateral view of the thorax of the female shows that the metanotum has fused with the propodeum. In *Cephalonomia quadridentata* the females are always wingless, but the males may be either winged or wingless; van Emden has carefully investigated the morphology of the three forms and his drawings illustrate a number of interesting points. The thorax of the wingless males demonstrates

very clearly, without the possibility that sexual dimorphism is implicated, the great reduction in size that the thorax may undergo on loss of the wings; van Emden has expressed this quantitatively in a table on page 443 of his paper. Another point that his figures illustrate is the loss of the pre- and postphragmas of the mesonotum in the wingless males; this is particularly striking in the postphragma, for in the winged males this extends to the back of the propodeum, but seems to be entirely or almost entirely absent in the wingless males. The same thing occurs in the winged and wingless males of the Chalcid *Trichogramma semblidis* (Auriv.) (p. 434). Van Emden's figures show the prepectus very plainly, but do not indicate any median ventral suture; it has not been possible to check this, for this portion of the prepectus is not visible in any of the specimens of *Cephalonomia* or *Scleroderma* that have been examined. In addition to *Mangesia* and allied genera (p. 403) this median ventral division of the prepectus has been observed in *Holepyris*, *Rhabdepyris*, and *Mesitius*.

The wingless females with much modified thoraces among the genera

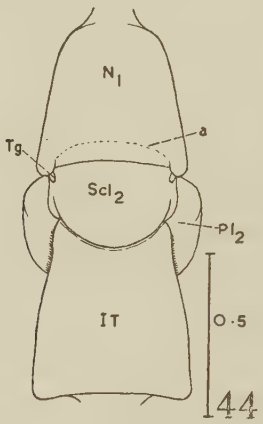


Fig. 44.—*Scleroderma domesticum* (Bethylidae), ♀, dorsal.

Cephalonomia, *Scleroderma*, *Parascleroderma* and *Ecitopria*, form a group in which the thorax is a little different from that of *Mangesia* and its allies though of the same type. The various features of the thorax (fig. 44) are less exaggerated than those of *Mangesia*; the mesopleura are less abruptly prominent and lack a well-defined dorsal surface, the propodeum is not so long and is without a narrow waist, and the spiracle—not visible in the figure—is about half-way along the side of the propodeum. The scutum and scutellum are fused and only a very faint depression marks the area of junction; as usual the scutum is reduced.

The resemblances between the Bethylidae and the Scoliiformes do not stop short at the striking similarities in the modifications of the thorax that have occurred in the wingless forms. The general appearance of the normal winged forms among the majority of Bethylid genera is very like that of many Scoliiformes. An analysis of this general impression shows that most parts of the body reveal a strong similarity in the two groups. The Bethylid thorax is very like that of *Tiphia*; this is particularly true of the propodeum both in shape and sculpturing, but much the same is true of the pronotum, the shape

and position of the meso-metapleural suture and the condition of the metapleuron. The oblong flattened head is like that of some TIPHIIDAE, and in the females of the BETHYLIDAE the thickened legs with expanded femora are like those of most female Scoliiformes. In the females of *Pristocera* and allied genera, the shape of the abdomen, as well as of the other parts of the body, is very like that of the wingless species of *Braunsomeria*. It is also significant that of the species of BETHYLIDAE whose habits are known, a high proportion are, like the Scoliiformes, parasites of beetle larvae. One cannot doubt that this section of the BETHYLIDAE has strong affinities with the TIPHIIDAE and Kieffer (1908), in his monograph of the BETHYLIDAE, expressed much the same opinion, considering them to be closely related to *Tiphia* and *Meria*. Ashmead (1902) expressed a very similar opinion, though he included among their relatives, in addition to what I have called the Scoliiforme families, his MYRMOSIDAE and MUTILLIDAE (Mutilliformes of this paper). I cannot see anything more than a very indirect relationship via the Scoliiformes, between the BETHYLIDAE and the Mutilliformes. Bridwell (1917) also regarded the BETHYLIDAE as having affinities with Scolioid forms.

Turning now to the second type of thorax, found in *Mesitius* and its allies, none of the species of *Mesitius* I have seen is entirely wingless and the thorax is only in the rather early stages of reduction and modification; thus in order to show that the modification is indeed of a different type from that of *Mangesia*, *Pristocera*, *Scleroderma*, etc., it will be better to describe first the thorax of a related form, *Promesitius coeruleus* Kieff. (fig. 45), in which modification has proceeded farther. The thorax of this insect (female) is modified along quite different lines from those of *Pristocera* and its allies. The most important difference is that the scutum, instead of being very much smaller than the scutellum, is larger; this difference is best seen by comparing the relative lengths of these sclerites in forms like *Mangesia* (fig. 42) and in *Promesitius* (fig. 45). It may be objected that this difference is merely due to a comparatively slight degree of thoracic modification in *Promesitius* compared with *Mangesia*, and that if *Promesitius* were more modified one might find the scutum becoming smaller than the scutellum; however, it can be shown that this is not so, for in the British Museum there is a specimen of an undescribed insect which is very like *Promesitius*, though evidently not belonging to the same genus. In this insect the wings have been entirely lost and thoracic modification has proceeded farther than in *Promesitius*, but the scutum has become larger, so that it is at least twice as long as the scutellum, whereas that of *Promesitius* is only half as long again. Further differences between *Promesitius* and the *Pristocera* type are that the mesopleura of *Promesitius* are not abruptly prominent, the propodeum is not elongated, and the posterior margin of the pronotum does not overlap the anterior border of the scutum. The metanotum is fused with the propodeum and its anterior margin is probably concealed under the scutellum; in the insect allied to *Promesitius* the metanotum appears as a transverse crenulate groove. *Mesitius*, by virtue of its relation to *Promesitius*, is almost certainly tending to the same type of thoracic modification, though the rather slight amount of modification that has occurred makes it difficult to demonstrate this clearly. However, one can say quite definitely that *Mesitius* is following a different line from *Pristocera* and its allies and the strong presumption is that this line is that taken by *Promesitius*. The most obvious difference between the thorax of the short-winged forms of *Mesitius* (fig. 46, *M. brevipennis* (Cam.)) and the thorax of forms allied to *Pristocera* or *Scleroderma*, in which modification has not proceeded very far, is

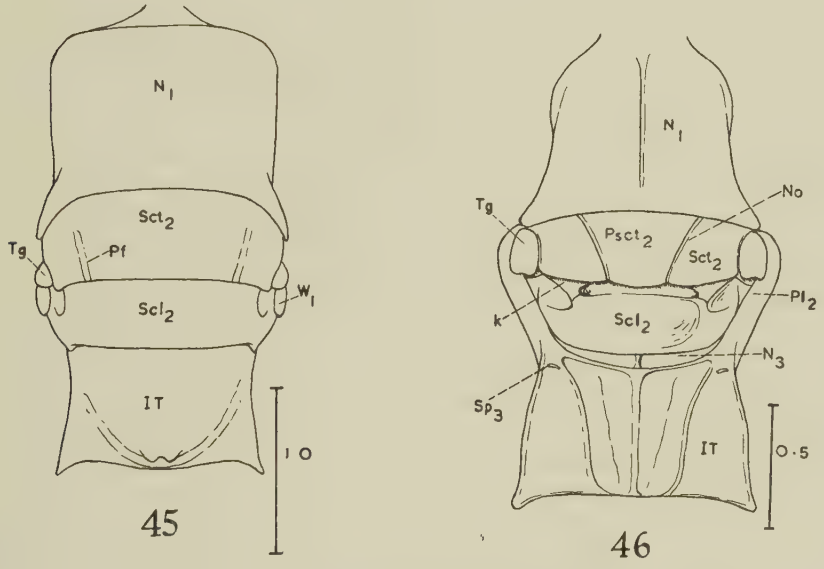
that in *Mesitius* the secondary sutures of the mesonotum (scuto-scutellar suture, notaulices, etc.) are better developed in the short-winged forms than in the normally winged. In the short-winged forms they are very heavily impressed. In forms allied to *Pristocera* these secondary sutures tend to be obliterated in the short-winged forms and as I have shown are entirely absent in the much-modified forms.

There are a number of genera containing wingless or subapterous forms, of which I have seen only specimens in which the modification of the thorax has not proceeded very far. Of these genera the appearance of the thorax in the flightless species of *Bradepyris* and *Rhabdepyris* is very similar to that of *Mesitius*, while the thorax of the flightless species I have seen in the genera *Arysepyris*, *Holepyris* and *Rysepyris* suggests that their affinities are with the more typical Bethylids. The appearance of other parts of the body confirms the testimony of the thorax; the head in *Bradepyris* and *Rhabdepyris* is somewhat rounded and the femora are not much dilated; both these conditions occur in *Mesitius*. The head in *Arysepyris* and *Rysepyris* is of the typical flattened and oblong Bethylid shape and in these two genera and in *Holepyris* the femora of the females are considerably dilated in the usual manner.

It is mentioned on page 402 at the beginning of this section on the Bethylidae that *Mesitius* is one of several genera that connect the Bethylidae with the Chrysididae. At first sight a connection between the Bethylidae and the very distinct Chrysididae does not appear likely, but I think the evidence is convincing and both Ashmead (1902) and Kieffer (1908) consider the Bethylidae to have affinities with the Chrysidids. Ashmead considers the Amiseginae and Cleptinae to be the forms which ally the Chrysididae to the Bethylidae; he mentions the extremely close similarity of the venation of these groups to that of many Bethylids, and in dealing with the Amiseginae he described a new species, *Mesitiopterus kahlii* Ashm., which he says has a venation like that of the Bethylid genus *Mesitius*. Börner (1919) regarded the Bethylidae and Chrysididae as connected by the Cleptidae. Bridwell (1917) also regarded the Bethylidae and Chrysididae as related. Since Ashmead's paper (1902), Kieffer has established two new genera of Bethylidae each containing several species: *Promesitius* (1905) (see above) and *Godfrinia* (1911). In his monograph of the Bethylidae (1914, *Das Tierreich*), Kieffer placed these two genera in the tribe Mesitiini, which is characterised by having the postero-dorsal angles of the propodeum toothed. This tribe contains the following genera, *Mesitius*, *Promesitius*, *Godfrinia*, *Saphobethylus* and *Harpagocryptus*. *Saphobethylus* has been shown by Turner and Waterston (1917) to be synonymous with *Olixon* Cam., and it has been recently shown that *Olixon* belongs to the Pompilidae (Reid, 1939); *Harpagocryptus* appears to be allied in some way to *Olixon*. This leaves *Mesitius*, *Promesitius* and *Godfrinia* which have real affinities with one another, but for reasons which are given below I am emphatically of the opinion that *Godfrinia* and *Promesitius* are Chrysidid genera.

Since Kieffer appreciated the fact that the Chrysidids and Bethylids are allied, it is difficult to see why he should have placed these two genera in the Bethylidae when the balance of characters so clearly puts them in the Chrysididae. In the case of *Promesitius* he appears to have been influenced by the fact that the abdomen is not concave beneath, and that the species, 4 of which are represented in the British Museum, are all wingless (all the individuals are females). The following are the more important characters that show that *Promesitius* should be regarded as a wingless Chrysidid genus having certain

affinities with the BETHYLIDAE through the Bethylid genus *Mesitius*. The head is like that of a Chrysidid, in particular of *Amisega*, and quite unlike that of a Bethylid; it is large, with very large eyes, and is widest across the vertex, narrowing to the base of the mandibles. The head between the eyes is longitudinally concave, the concavity transversely wrinkled; the 13-segmented antennae are inserted close to the ventral margin of the head, they are strongly elbowed and the flagellum is fusiform. The clypeus is short and longitudinally carinate medially. The head of *Mesitius* is not oblong and flattened like that of a typical Bethylid, but is somewhat pear-shaped, broadest dorsally; the clypeus is longitudinally carinate. The thorax of *Promesitius* has already been discussed, and it has been shown that the type of modification which it has undergone is different from that which takes place in the typical wingless



FIGS. 45–46.—45, *Promesitius coeruleus* (BETHYLIDAE), ♀, dorsal; 46, *Mesitius brevipennis* (BETHYLIDAE), ♀, dorsal.

Bethylids. Both head and thorax are heavily rugosely punctured in the manner typical of the Chrysidids and in the 4 species I have seen the head is metallic and in 3 of them also the thorax. There are several points of similarity in the thoraces of *Mesitius* and *Promesitius*; in both the pronotum bears a median longitudinal furrow, and the postero-dorsal angles are produced and divergent (figs. 45 and 46). The condition of the prepectus is similar, very clearly sutured from the mesopleura. The postero-dorsal teeth on the propodeum are the most obvious features of similarity and are characteristic of the CHRYSIDIDAE. The semi-circular furrow on the propodeum of *Promesitius* is also present in *Cleptes* though less well defined. The abdomen of *Promesitius* is very Chrysidid-like; only about 4 segments are visible dorsally and of these the first 2, which are partially fused, form almost the whole of the dorsal surface of the abdomen. Though the ventral surface is not concave it meets the dorsal surface at an angle, so that the lateral margin of the abdomen is sharply defined; the terminal segments are apparently tubular as in Chrysidids,

It is evident that *Promesitius* has no important Bethylid characters, and though it shares certain characters with *Mesitius* these do not demonstrate Bethylid affinities in *Promesitius*, but rather Chrysidid affinities in *Mesitius*. Nevertheless, I am satisfied that *Mesitius* is really a Bethylid genus, for apart from those Chrysidid affinities mentioned above, its other and more important characters are those of a Bethylid; in particular the abdomen has 6 or more segments visible dorsally instead of 5 or fewer as in Chrysidids.

In the next few paragraphs I shall digress a little from my main subject, but the problems discussed in these paragraphs arose during the investigation of the connection between the Chrysididae and Bethylidae, which in turn was prompted by examining the wingless thorax of *Promesitius*. Kieffer (1911) in his description of the genus *Godfrinia* makes no mention of its Chrysidid affinities and places it without comment in the Bethylidae; whilst in describing *Promesitius* (1905) he noticed its affinities to the Chrysididae and even expressed doubt as to whether it is a Bethylid. This is rather surprising, because although the Chrysidid-like characters of *Promesitius* are clearly evident, it appears to be very distinct from any of the established genera of Chrysidids and would probably have to be placed in a new subfamily; whereas a comparison of the species of *Godfrinia*, of which there are three represented in the British Museum, with those of *Cleptes*, shows that they are no more than generically distinct from *Cleptes*. Although the species of *Godfrinia* have much less metallic colouring than those of *Cleptes*, they always show a little, usually on the head; the antennae are 13-segmented in both sexes; the pronotum has the transverse furrow characteristic of *Cleptes*, and the abdomen is closely similar. The differences are relatively small and among them one may mention the following: the pronotum of *Godfrinia*, in addition to the transverse furrow or fold, bears a median longitudinal one as in *Mesitius*; this is lacking in the species of *Cleptes* I have examined. The shape and sculpturing of the propodeum and the size of the teeth on the terminal angles are different in the two genera. It seems, then, that the proper position of *Godfrinia* is in the Cleptidae.

Brues (1910) discussed the affinities of the Bethyloidea and expressed the opinion that the Bethylidae, through such genera as *Epyris* and *Pristocera*, have been derived from the Ampulicidae, in particular from some form like *Rhinopsis*. This opinion has led me to examine a number of species of *Ampulex* and the examination reveals the interesting fact that *Ampulex* seems to have a number of characters in common with such forms as *Cleptes* and *Mesitius*. In many species of *Ampulex* the propodeum is very like that of *Mesitius* (fig. 46); there are teeth at the postero-dorsal angles, a rim round the dorsal margin, and a similar pattern of longitudinal ridges, while the spiracle occupies a similar position. The mesonotum has notaulices, which is a Bethylid-like character. The pronotum, which is often elongate and somewhat peculiar in shape, is nevertheless of the same type as that of *Cleptes* and *Godfrinia*; the postero-dorsal angles are produced into a lobe which stretches towards the tegulae, and in a less marked fashion the same thing occurs in *Cleptes*; these angles are divergent when viewed from above; there is a transverse furrow and sometimes also a longitudinal one. What may be an important character is to be found in the metasternum, which in *Ampulex* is somewhat peculiar; medially it is raised into two parallel longitudinal ridges with a furrow between in which the furcal pit is situated; posteriorly these two ridges diverge and form a pair of tongue-like processes which overlie a part of the base of each hind coxa. In *Cleptes* and *Godfrinia* the metasternum is of the same structure, though as in

the case of the pronotum, less pronounced than in *Ampulex*; the furrow is shallow and the processes are small. It should be remarked that a metasternum, similar to that of *Ampulex*, exists in some of the true SPHECIDAE. There are other suggestive points; for example, the dorsal aspect of the abdomen of some male AMPULICIDAE is distinctly Chrysidid-like, there being only about 4 segments visible and the second being much the largest. The colour of *Ampulex* is usually metallic green; the clypeus, though having other peculiarities as well, is longitudinally carinate. There is a distinct tendency throughout the family for the wings to undergo a small amount of reduction in size. In the light of this evidence the affinities of the AMPULICIDAE obviously require further investigation; they are usually associated with the Sphecids and if they have real affinities with the latter they would seem to connect the Sphecoids and Vespoids.

To sum up this discussion of affinities: there are several genera among the BETHYLIDAE, CHRYSIDIDAE and CLEPTIDAE which indicate a fairly close connection between these three families and probably other such genera await discovery.[1] The result is that it is not easy to find critical characters for separating the BETHYLIDAE from the Chrysidid-like forms, though perhaps the number of abdominal segments visible from above (6 or more in the Bethylids, 5 or fewer in the Chrysidids and Cleptids) and the condition of the terminal segments (whether tubular or not) might prove satisfactory. A brief summary of some of the opinions that have been expressed regarding the affinities of the BETHYLIDAE is given by Wheeler (1928).

(ii) DRYINIDAE.

In contrast to the BETHYLIDAE, the thorax of the DRYINIDAE has yielded very little phylogenetic information. The unmodified winged thorax seen in all the subfamilies in the males, and in the APHELOPINAE in the females also, bears no particular resemblance to the thorax of the BETHYLIDAE. As to the wingless thorax, that of the females of the GONATOPODINAE is very highly modified, but in a manner peculiar to the DRYINIDAE and unlike that of any other group of wingless Hymenoptera. Moreover there can be little doubt that these modifications are in a large measure adaptive, being concerned in the raptorial habits of the insects, and are not solely due to modification consequent upon the loss of wings. I do not mean to suggest that in other groups of wingless Hymenoptera the modifications have no functional significance, for this is almost certainly not the case; consider, for example, the increased

[1] Since writing this I have seen a series of specimens, containing about four species, collected by R. E. Turner in Pondoland, Zululand and Cape Province. These are as yet undescribed and form a genus allied to *Promesitius*, and most closely allied to the undescribed insect referred to on page 405 which is from Zululand, but may be generically distinct.

There is thus a very distinct group of related forms, which to my knowledge contains about three genera and ten species; *Promesitius* in Australia with about five species, and these two undescribed genera from Africa, one with about four species and the other with one. The group should probably be regarded as a new subfamily of highly aberrant Chrysidids which through *Promesitius* shows some affinities to the Bethylid genus *Mesitius*. Of the group, *Promesitius* is the most Chrysidid-like and has the least highly modified thorax, while the insects collected by Turner have the most modified thorax and are the least Chrysidid-like, though they still retain a little metallic coloration, particularly on the head. But for the resemblance of the latter to *Promesitius* one might at first fail to note their Chrysidid affinities. The characteristics of the thorax of this group are: progressive elongation of the pronotum, shortening of the propodeum and growth of the scutum with corresponding reduction of the scutellum.

prominence of the mesopleura in wingless female Bethylids such as *Pristocera*, which is probably at least in part correlated with the increase in size of the middle legs, serving to accommodate the larger coxal muscles. But in the Gonatopodinae the apparently adaptive modifications are very much more striking than in other wingless forms, and for the very reason that they are adaptive they have, for the present purpose, little comparative value outside the Dryinidae.

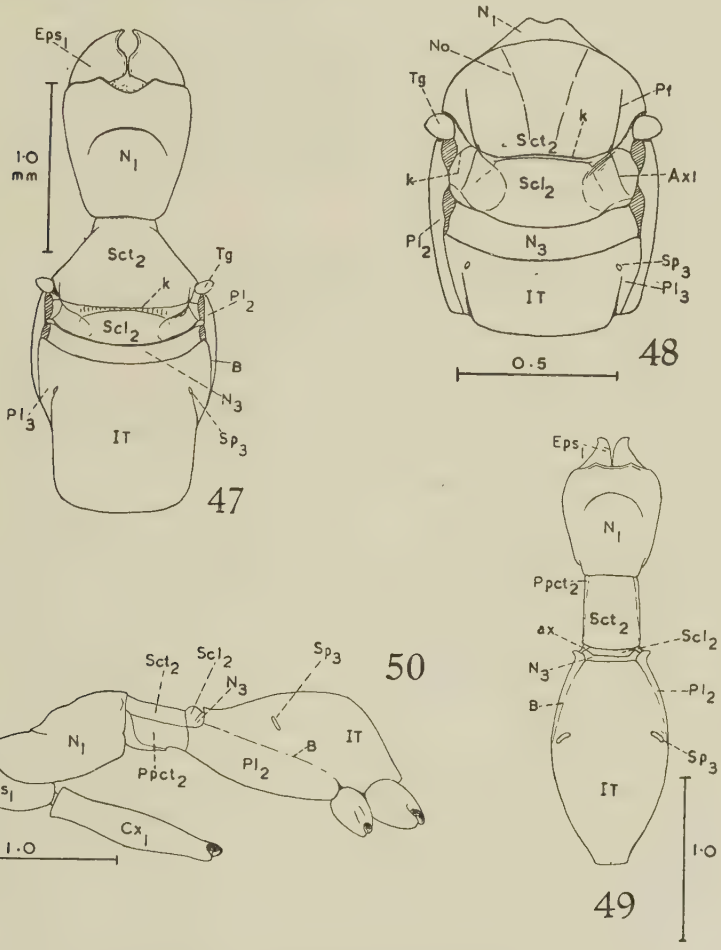
Fig. 47 shows a dorsal view of the female thorax of *Neodryinus koebelei* Perk. It is fairly typical of the subfamily Dryininae in which the females, with the exception of about three species, are all winged and yet have the thorax very considerably modified in connection with their raptorial habits. This modification is possible because it affects mainly the prothorax, while the mesothorax, which is the important wing-bearing segment, is only slightly involved. Anteriorly the mesoscutum is narrowed to form a short petiole where it joins the pronotum. The latter is large and much specialised and together with the proepisterna forms a functionally separate segment, instead of being, as is normally the case, subordinated to the requirements of the mesonotum. Dorsally the pronotum bears a curved transverse furrow which is a characteristic feature of the females of the Dryininae and Gonatopodinae. The anterior margin of the pronotum is widely separated from the head, which articulates solely upon the enlarged proepisterna that intervene between it and the pronotum. This arrangement doubtless increases the mobility of the head, while the enlargement of the episterna and of the pronotum is certainly in part connected with the increased size of the forelegs, particularly the coxae (see fig. 54). It seems that in some, if not all Bethylids, the pronotum takes no part in the articulation of the head.

Comparison of the female thorax of *Neodryinus koebelei* (fig. 47) with that of the male (fig. 48) emphasises the degree of specialisation that the thorax of the female has undergone. The figures show that the mesonotum (and therefore presumably the powers of flight) of the male is much more developed than that of the female; this is a common form of sexual dimorphism.

Fig. 49 is a dorsal view of the female thorax of *Gonatopus testaceus* Cam. All the females of the subfamily Gonatopodinae (except *Echrodelphax*) are wingless and this figure shows that the thorax has been modified along the same lines as in *Neodryinus koebelei* (fig. 47), but that the modifications have proceeded much farther. The pronotum and episterna are very much the same as before; but the mesothorax, released from subservience to the function of flight, has become very much modified and specialised. It now forms a long and slender waist connecting the pronotum and the bulky posterior part of the thorax. The dorsum of the mesonotum is formed almost entirely of the scutum, while the scutellum is much reduced. A transverse groove between the scutellum and the propodeum is probably the metanotum which is more often fused with the propodeum. The lateral view (fig. 50) displays the structure of the thorax more completely. The most interesting feature is the prepectus, which has assumed considerable importance as it forms the lateral and ventral walls of the mesothoracic waist; the early stages in this specialisation of the prepectus can be seen in the female thoraces among the Dryininae. The hind margin of the mesopleuron is faintly marked while the metapleuron is indistinguishably fused with the propodeum.

Among the various modifications of this thorax, there is one that may possibly have some phylogenetic significance; this is the enlargement of the scutum and the reduction of the scutellum. This condition may perhaps be

regarded as a non-adaptive one as there seems to be no good reason why the reverse should not have occurred and it would have obviated the necessity for the unusual specialisation of the prepectus. On the assumption that this particular condition of the scutum and scutellum is not closely adaptive, one may use it for purposes of comparison. It may be remembered that in the wingless Bethylidae allied to *Pristocera* and *Scleroderma*, the scutum becomes



Figs. 47–50.—47–48, *Neodryinus koebelei* (Dryinidae), 47, ♀, dorsal; 48, ♂, dorsal; 49–50, *Gonatopus testaceus* (Dryinidae), 49, ♀, dorsal; 50, ♀, lateral.

reduced while the scutellum remains large; the inference is that if the Dryinidae have any affinities with the Bethylidae, one would expect them to be with *Mesitius* and allied genera where there is the same tendency for the scutellum to be reduced, rather than with such forms as *Pristocera*.

Brues (1910) described and figured a new species under the name *Dryinopsis simplicipes* and assigned it to the Dryinidae. It seems extremely unlikely that it can be a Dryinid, of which it lacks the most important characters. The specimen is a female and wingless, with a highly modified thorax which bears a

superficial resemblance to that of *Gonatopus*. The antennae are 12-segmented; those of the DRYINIDAE are always 10-segmented in both sexes. The fore tarsi are simple and non-chelate, a condition that only occurs among female Dryinids of the subfamily APHELOPINAE, which are always winged. There is no elongation of the fore coxae as in wingless female Dryinids. There is a number of characters in which the thorax appears to differ from that of the GONATOPODINAE. It appears from the figure that the head articulates with the pronotum, certainly the latter is shown as reaching the back of the head, while in the typical DRYINIDAE the pronotum is widely separated from the head. There is no sign of the characteristic development of the proepisterna seen in Dryinids. The scutellum is much larger compared with the scutum than in the GONATOPODINAE and the meso-metapleural suture is in a quite different position, being far shorter and more nearly vertical; this last feature is correlated with the fact that the second coxae are much more anterior in position than in *Gonatopus*.

The thorax of *Dryinopsis simplicipes* appears to be very similar to that of the species of *Methoca* described by Williams (1919) in which the scutum is flat so that the anterior part of the mesothorax is stalk-like; there is just the same pattern of longitudinal striations on this part of the thorax in *Dryinopsis* as in these species of *Methoca*. *M. punctata* Wllms., of which I have seen a specimen, is very like the figure of *Dryinopsis*. Brues noted the similarity to *Methoca* but considered it to be superficial; admittedly the shape of the head in the figure appears to be rather unlike that of a *Methoca*. The maxillary palps are 5-segmented; so far as I know those of the species of *Methoca* have 6 segments.

Kieffer (1914) placed *Dryinopsis* in the BETHYLIDAE, where it appears to be just as much out of place as in the DRYINIDAE. The possibility that it is related to *Methoca*, if not actually a species of *Methoca*, should be re-examined. If it has lateral prepectal sclerites concealed beneath the pronotum, metathoracic spiracles like those of many worker ants, and a pair of small tooth-like processes on the back of the mesosternum, then it certainly belongs with *Methoca*. The prepectal sclerites are very difficult to see unless the fore coxae are considerably displaced.

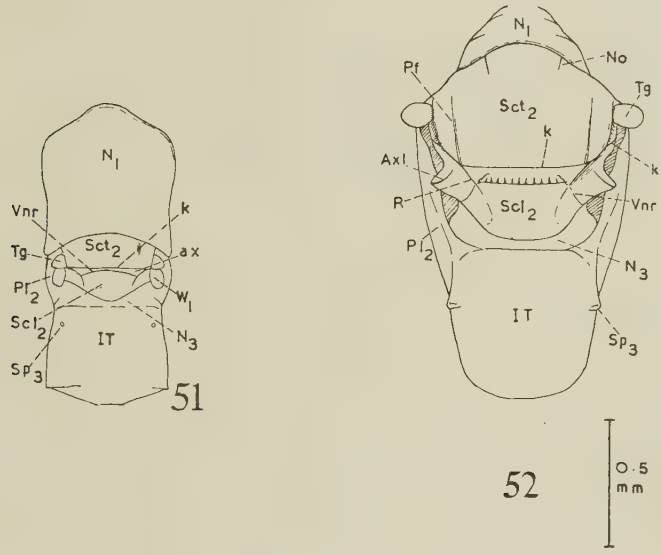
(iii) EMBOLEMIDAE.

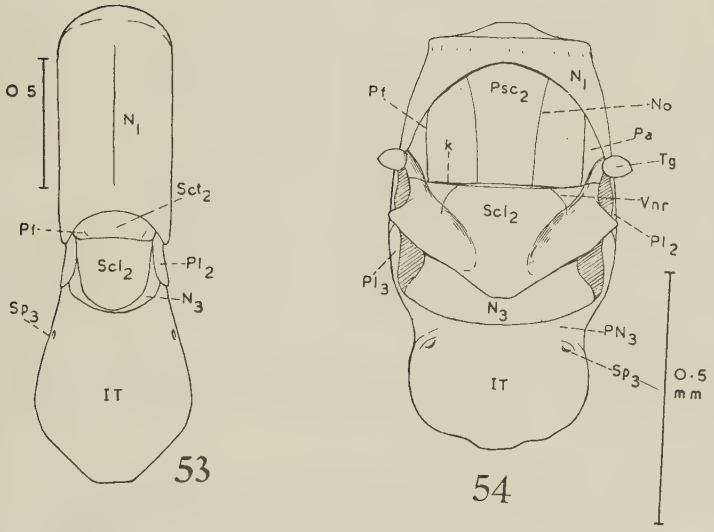
This is a family of a few rare species, in which the females are all wingless or short-winged. Fig. 51 shows a dorsal view of the female thorax of *Embolemus* sp. The chief features of this thorax are the large size of the pronotum, which has a slight longitudinal median furrow, and the small size of the mesonotum, which nevertheless retains all its parts unfused and of much the same shape and size, relative to one another, as in a normal thorax; when the mesonotum becomes as small as this it usually undergoes considerable modification. The mesopleura are not prominent and the thorax bears no obvious resemblance to that of the BETHYLIDAE. The thorax of *Embolemus ruddii* Westw. ♀, is closely similar to that of *E.* sp. Fig. 52 shows the dorsal aspect of the thorax of the male *Embolemus ruddii* Westw.; the figure emphasises the great development of the pronotum that has taken place in the female.

(iv) SCLEROGIBBIDAE.

This is another family with a few rare species in which the females are all wingless. Fig. 53 is a dorsal view of the female thorax of *Sclerogibba rufithorax* (Cam.). It is more modified than that of *Embolemus*; the pronotum is of very

great size and this is undoubtedly correlated with the great size of the forelegs, the femora of which are enormous. The same applies to the proepisterna.





FIGS. 51–54.—51, *Embolemus* sp. (EMBOLEMIDAE), ♀, dorsal; 52, *E. ruddii*, ♂, dorsal; 53, *Sclerogibba rufithorax* (SCLEROGIBBIDAE), ♀, dorsal; 54, *Probethylus callani* (SCLEROGIBBIDAE), ♂, dorsal.

The pronotum does not reach to the back of the head, dorsally it has a median longitudinal furrow. The mesonotum displays considerable modification and is composed largely of the scutellum, the scutum being considerably reduced though it still retains parapsidal furrows. The sclerite intervening between the

scutellum and the propodeum is probably the metanotum, in which case its relation to the mesopleuron is a little unusual. The mesopleura do not project at all. *Probethylus callani* Rich. is very similar, but the metanotum is less clearly defined and the scutellum is considerably convex while that of *Sclerogibba rufithorax* is somewhat flattened. The thorax of the male Sclerogibbid (fig. 54, *P. callani*) is very different from that of the female. In the thorax of the female the reduction of the scutum suggests an affinity with the main group of the Bethylidae or with the Scoliiformes, but this does not seem to be borne out by any other feature of the thorax. The longitudinal furrow on the pronotum occurs also in the Embolemidae (fig. 51), in *Mesitius* (fig. 46), *Promesitius* (fig. 45), *Godfrinia* and many Ampulicidae.

(v) Interrelationships of the families of the Bethyloidea.

Brues (1910), in the paper already referred to, considered the Dryinidae as well as the Bethylidae to have been derived from Ampulicid types; he considered the Embolemidae to be related to the forms from which the Proctotrupoidea are descended and considered the Sclerogibbidae to be related to the Tiphiidae and Anthoboscidae (Cosilidae). The interrelationships of the Bethylidae, Chrysididae, Cleptidae and Ampulicidae have already been considered (p. 408). A study of the wingless thorax of the Dryinidae does not seem to reveal any obvious relationships with other groups (p. 409). The thorax of the females of the Sclerogibbidae may perhaps indicate a distant relationship with such forms as the Tiphiidae, in particular because of the reduction of the scutum; the shape of the pronotum in the males is somewhat like that of the males of the Scoliiformes. However, these slight apparent affinities could equally well be with the main group of the Bethylidae. The Sclerogibbidae are so specialised that they must have been a distinct group for a very long time, consequently one might expect that they would show slight affinities with several different groups and close affinities with none. All that one can do in such cases, and they are numerous, is to try to estimate with which group such isolated forms have the greater number of characters in common and then to place them accordingly. There is probably a connection between the Sclerogibbidae and the Embolemidae; the thoraces of the females have certain features in common; for example, the long pronotum with its median dorsal furrow and the non-projecting mesopleura. The Embolemidae probably have some affinities with the Dryinidae, the thorax of the males of the Embolemidae being more like that of the male Dryinids than any other families of the Bethyloidea. Perkins (1905) evidently considered the Dryinidae and Embolemidae to be related and looked upon them as intermediate between the Proctotrupoidea and the older forms among the Fossores.

Material examined in the Bethyloidea.

Bethylidae.—*Mangesia incerta* Turn., *M. atopogamia* Turn., *Scleroderma domesticum* Latr. *et al.*, *Mesitius brevipennis* (Cam.) *et al.*, *Promesitius coeruleus* Kieff. *et al.*, *Sierola* spp., *Pristocera*, *Pseudisobrachium*, *Apenesia*, *Arysepyris*, *Holepyris*, *Rysepyris*, *Rhabdepyris*, *Bradepyris*, *Cephalonomia*, *Ecitopria*, *Parascleroderma* spp.

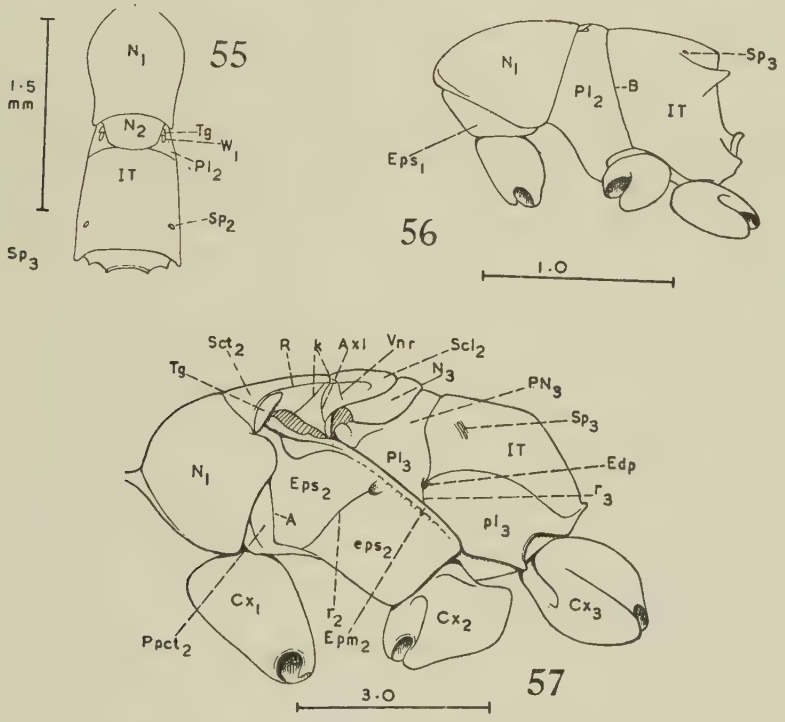
Dryinidae.—*Mystrophorus formicaeformis* Ruthe, *Neodryinus koebelei* Perk., *Gonatopus testaceus* Cam., *G. palliditarsus* Cam. *et al.*, *Dryinus* spp., *Anteon* spp. etc.

Embolemidae.—*Embolemus* sp., *Embolemus ruddii* Westw.

Sclerogibbidae.—*Sclerogibba rufithorax* (Cam.), *Probethylus callani* Rich.

14. Pompilidae.

In this large family there are a few wingless and short-winged forms and in a number of these the male has the wings as much reduced as the female. Fig. 55 shows a dorsal view of the thorax of the male of *Psyllosphex dentatus* (Cam.). It will be seen that the mesonotum has become greatly reduced, while the pronotum and propodeum have become longer. Much of the growth of the propodeum appears to have occurred in the anterior half, because the spiracle is displaced posteriorly compared with its position in winged Pompilids (fig. 57). The scutum and scutellum of the mesonotum have become indistinguishably fused together; but the condition in other species of *Psyllosphex* (Arnold, 1935)



Figs. 55–57.—55–56, *Psyllosphex dentatus* (Pompilidae), 55, ♂, dorsal; 56, ♀, lateral; 57, *Hadropompilus montanus* (Pompilidae), ♀, lateral.

in which they are still distinct shows that there has been no large alteration in the relative sizes of the two areas. The metanotum is hardly distinguishable; medially it is represented by a narrow groove between the scutellum and propodeum. The mesopleura are somewhat concave. Fig. 56 shows a lateral view of the female thorax of *Psyllosphex dentatus* which may be compared with fig. 60 of the thorax of the female of *Hadropompilus montanus* Arn.; these figures emphasise the great reduction in size that the mesothorax of *P. dentatus* has undergone. It will also be seen that the mesopleuron has lost the division into dorsal and ventral portions and that the epimeron is no longer visible; the endophragmal pit now lies close against the meso-metapleural suture, while that between the metapleuron and propodeum has disappeared.

Except for minor details the condition of the thorax in *Apteropompiloides leptosomus* Arn., and *A. tosquineti* Brauns, is the same as that of *Psyllosphex dentatus*. The pronotum of these two species, which are quite wingless, is relatively longer than that of *P. dentatus*; the propodeal spiracle is not displaced so much posteriorly; the metathoracic spiracles, not visible in *P. dentatus*, are obvious in *Apteropompiloides* and are much like those of the workers of many species of ants, each being guarded by a small circular sclerite. In *A. leptosomus*, though the scutum and scutellum are fused, the limits of each can be made out as there is a slight transverse shallow depression marking the area of junction; there has been no reduction of the scutum and growth of the scutellum or *vice versa*. There are several genera such as *Sphictostethus*, *Haploneurion*, *Dromocharis*, *Pseudopedinaspis*, etc., in which short-winged forms occur, but in these the modification of the thorax has hardly commenced, beyond the usual reduction in size of the mesothorax.

When considering whether the thorax of the wingless Pompilids throws any light on the affinities of the family, one cannot help noticing the similarity that exists between the thorax of *Psyllosphex dentatus* (fig. 55) and that of *Embolemus* (fig. 51). The mesonotum of the former is more reduced and modified than that of the latter, but as already mentioned other species of *Psyllosphex* (Arnold, 1935) have the mesonotum in the same condition as *Embolemus*. In addition to the similar type of modification in the two genera, there are similarities in detail, such as the shape and size of the propodeum and pronotum and the angle made by the meso-metapleural suture. If there is a true connection between the Pompilidae and the Embolemidae, it must be a distant one, for the structure of the normal Pompilids is very unlike that of the Embolemidae which, moreover, are presumably parasitic. It appears, however, that there may be certain forms which will help to bridge this wide gap. I have shown recently (Reid, 1939) that *Olixon testaceum* Cam. is a Pompilid allied to *Psyllosphex* [2]; the general appearance of this insect is at first sight unlike that of a Pompilid and it is perhaps significant that in the past it has been considered to be an Embolemid (Ashmead, 1902). There are several genera apparently related to *Olixon* and *Psyllosphex*, and one of these, *Harpagocryptus* Perkins, was reared from a cricket on which the larva had formed a sac like that made by many Dryinids. If *Olixon* and some of its allies behave as parasites, then one of the greatest obstacles to believing in a connection between the Pompilids and Embolemids is removed. At present the evidence for a connection between these two families rests upon the rather generalised structural resemblances referred to above; these might be due to convergence.

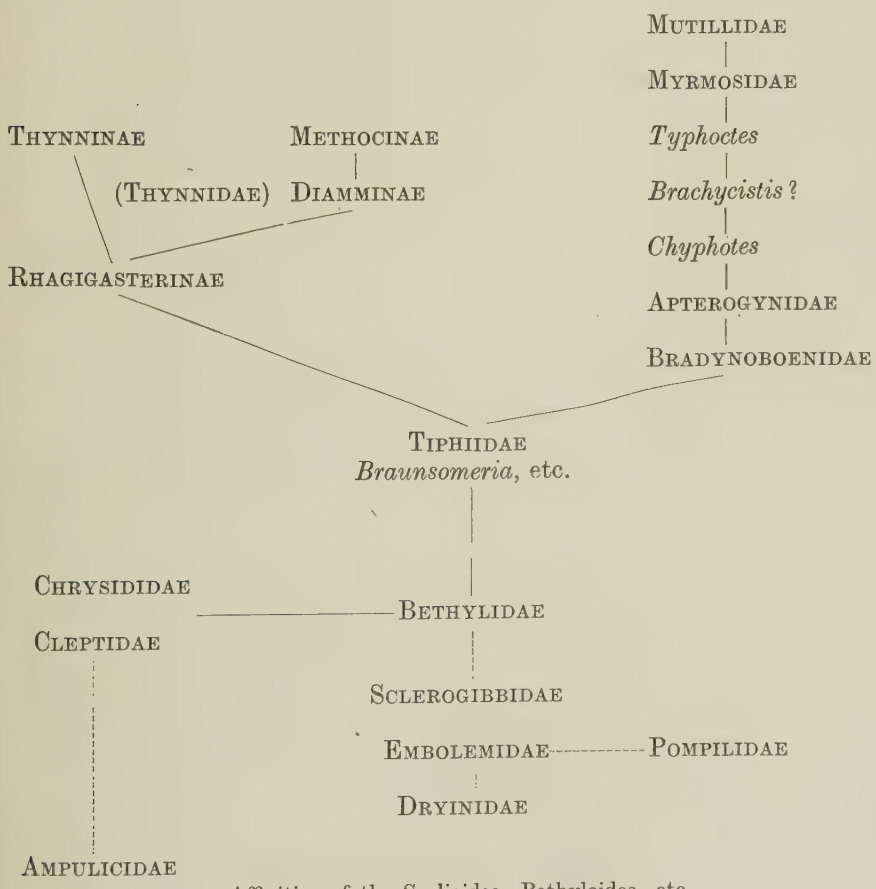
Various authors have considered the Pompilidae to be more closely related to the Sphecoidea than to the families which form Ashmead's Vespoidea; however, the occurrence of winglessness among the Pompilidae seems to indicate affinity with the Vespoidea, for I know of no cases of aptery among the true Sphecoids. There are a few forms allied to *Miscophus* that show a small degree of brachyptery, but the thoraces of these are unmodified (Arnold, 1923). Some Ampulicidae are brachypterous, but then it is by no means certain that this family belongs amongst the Sphecoids. The occurrence of aptery amongst the males as well as the females of some species of Pompilids is a rather exceptional feature.

[2] On re-examination with a higher magnification I have been unable to detect any crenulations in the groove separating the first and second abdominal segments in *Psyllosphex dentatus* and in consequence my figures and the text are in error with regard to this character. The presence of these crenulations is given by Arnold (1935) in his generic diagnosis of *Psyllosphex*, but *P. dentatus* is evidently exceptional.

15. Summary of the affinities of the Scolioids, Bethyloidea, Pompilidae, etc.

The accompanying diagram is a convenient summary of the relationships discussed in the previous pages. Only the groups dealt with in those pages are included. The broken lines indicate doubtful affinities. No attempt is made to indicate the limits of superfamilies, because many groups have not been studied, as no wingless forms occur among them. However, there is one superfamily that ought to be mentioned here; that is the Tubulifera containing the Chrysididae and Cleptidae. Wheeler (1928 : 55–56) makes use of it in the simple and fairly satisfactory classification which he proposed. The Chrysididae and Cleptidae are more obviously allied to the Bethylidae than are the Sclerogibbidae, Embolemidae and Dryinidae; consequently if these last three families are to be included with the Bethylidae in a superfamily Bethyloidea, then the Chrysididae and Cleptidae should also be placed in this superfamily.

One more point requires to be mentioned. It will be seen that the Tiphiidae occupy a central position in the diagram, and it may be remembered that the thoraces of the wingless females of such forms as *Pristocera*, *Braunsomeria*, and the Rhagigasterine Thynnids are extremely similar and that these forms have many other characters in common. Furthermore it has been shown that



Affinities of the Scolioidea, Bethyloidea, etc.

Bradynoboenus appears to connect the Mutilliformes with the Scoliiformes through such forms as *Braunsomeria*. The inference is that all these forms had a common ancestor which must have been very Tiphiid-like. This conclusion is based entirely upon the evidence presented in the foregoing pages and is therefore an independent one. Thus it is most interesting to find that Wheeler (1928) comes to the conclusion, by a process of elimination, that the TIPHIIDAE are probably the closest among living forms to the ancestors of the FORMICIDAE. He said: "It seems to me that the group which deserves the most serious attention in connection with the ancestry of the ants is the TIPHIIDAE and especially the genus *Elis* (*Myzine*). It is interesting to note that this very family TIPHIIDAE has affinities in structure and habits with the BETHYLIDAE considered in a former lecture. Probably all three convergent groups, the BETHYLIDAE, TIPHIIDAE and FORMICIDAE, had a common origin amongst extinct forms, which may be conceived to have resembled the existing Bethylids in habits." It seems, then, that one may postulate, with a reasonable degree of certainty, the former existence of a single Tiphiid-like ancestor for the FORMICIDAE and at least half of Ashmead's Vespoidea.

16. FORMICIDAE.

In dealing with the ants a direct comparison between the classification based on a study of the worker thorax and that based on other characters has not been made; instead I have used the method employed by Tulloch (1935), which is to compare the conclusions derived from a study of the thorax with an existing scheme of classification of the ants (Wheeler, 1922 and 1928).

I follow Snodgrass' interpretation of the thorax of the ants (1910) and not that of Emery (1900). I think there is a small error in Snodgrass' interpretation of the worker thorax of *Pogonomyrmex transversus* (Smith); the faint line which he took to be the scuto-scutellar suture is really that between the mesonotum and metanotum, for it will be shown later that the mesonotum of worker ants lacks any divisions; the area he labelled scutellum is therefore the metanotum.

Tulloch's paper on the thorax of the ants (1935) is largely devoted to the winged forms and deals only rather briefly with the worker thorax. He also follows Snodgrass and gives a review of the literature on the thorax of ants.

The thorax of worker ants displays great diversity, and all conditions exist from the relatively unspecialised, where the pronotum is free or nearly so, and the mesonotum, metanotum, and propodeum are all fairly clearly delimited from one another, to the highly modified type in which all parts of the dorsum have been fused into one convex surface and all or almost all traces of dorsal sutures have been lost. The actual volume of the thorax compared with the total volume of the body is probably smaller in some of the ants, *e.g.* soldiers of *Pheidole*, than in any other wingless Hymenoptera, and it appears in some forms as if the thorax is of the minimum size necessary to serve as an attachment for the coxae. In the more curiously shaped ants, the thorax, in company with other parts of the body, is frequently much modified. In very slender forms, such as species of *Odontomachus*, it is much elongated; when in addition the mandibles are very long, one may suspect that some of these species have raptorial habits. This may well be true of the curious genus *Myrmoteras*, of which I have seen a worker of *M. binghami* Forel. The appearance of the thorax and the apparently high degree of mobility of the head with its large eyes are characters distinctly suggestive of the condition seen in *Gonatopus* (DRYINIDAE); the function of the chelate fore tarsi of

Gonatopus is probably fulfilled by the long jaws of *Myrmoteras*. Creighton (1930), in an illustrated review of the genus, discussed the similarity of the jaw mechanism to that of other genera with long jaws such as *Harpegnathos* and *Strumigenys* in which jumping or retrosalience is common. He suggested that retrosalience may be a secondarily acquired habit and supposed that in *Myrmoteras*, whose habits are unknown, the jaws are probably adapted to catching active insects. Many of the species of *Polyrhachis* have enormous spines on the thorax and petiole and often those of the workers are larger than those of the winged females; this is well seen in *Polyrhachis lamellidens* Sm. The workers of this species, in addition to having spines that are larger than the corresponding ones in the winged females, have a large pair upon the mesonotum that are not present at all in the females. Certain species of *Cremastogaster*, e.g. *C. inflata* Sm., have the hind part of the thorax, in particular the propodeum, much inflated, apparently to accommodate the very large metapleural gland. As Tulloch points out, " metasternal " is incorrect as the gland opens on the metapleuron. The species of *Cryptocerus* and allied genera have the dorsum produced into a flange all round the perimeter of the thorax.

In all these forms in which the thorax is of an unusual shape, it nevertheless conforms to the normal subfamily or tribal type; thus the thorax of a worker of *Cryptocerus* is of the normal Myrmicine type.

In the following paragraphs the characters of the worker thorax in the different subfamilies of the ants are dealt with. A number of the species figured are the same as those figured by Tulloch (1935), and as the figures are nearly all dorsal views while Tulloch's are lateral, they are supplementary to his.

Ponerinae.

This subfamily is considered to be the most primitive one, from which the others are thought to have arisen; thus it is interesting to find that the thorax is more variable than in any of the other subfamilies, and that all conditions found in these have a parallel among the Ponerinae. In the other subfamilies, except the Dorylinae, the type of worker thorax is the same throughout the subfamily, but in the Ponerinae the type of thorax is not uniform, even within the limits of a tribe. This is significant in view of the opinion expressed by Wheeler (1910): " . . . that the Ponerinae comprise a number of different tribes, and this number will undoubtedly be augmented, when the subfamily has been carefully studied, beyond that of any of the other subfamilies."

Tribe Myrmeciini.

The thorax is relatively unspecialised and dorsally all the main regions can be distinguished. In *Myrmecia sanguinea* Sm. (fig. 58) the pronotum is separated from the mesonotum by a well-marked suture. The mesonotum is convex and without any trace of secondary divisions. The metanotum is represented by a depressed transverse area not bounded by any obvious sutures. The second or metathoracic pair of spiracles is large. The condition of the pleura is typical of that of the majority of worker ants; the mesopleuron is not divided into dorsal and ventral portions, the epimeron is suppressed, and the suture between the meso- and metapleura is present and that between the metapleuron and propodeum is not. The condition in *Pristomyrmecia fulvipes* (Roger) is the same in principle as the foregoing and differs only in secondary detail; the parts of the dorsum are less rounded and the metanotum is reduced

to a deep groove between the mesonotum and propodeum; this is the meso-epinotal suture of myrmecologists who refer to the propodeum as the epinotum.

Tribe Amblyoponini.

Myopopone castanea (Sm.) (fig. 59). The thorax is much more rectangular than in the Myrmeciini. The dorsum is considerably flattened and the mesonotum is reduced to a small transverse area, very short and small in *M. picea* Donisth. The metanotum is represented by a suture-like groove. Owing to the reduction in length of the mesonotum, the mesopleuron is narrow dorsally. The metathoracic spiracles are well developed, but are a little displaced ventrally. The other genera in this tribe differ in various points of detail. In *Amblyopone* the mesonotum is not quite so small and the metanotum is not so suture-like. The metathoracic spiracles are very reduced and there are faint signs of the division of the mesopleuron. In *Stigmatomma* the tendency is for the metanotum not to be depressed, but to be level with the propodeum and to fuse with it. A cross-section of the thorax would show that the dorsum is very convex and this results in the metathoracic spiracles appearing to be about one-third the way down the side of the thorax in the pleura, whereas in reality they are almost certainly on the line of junction of the dorsum and pleura, their usual position.

Tribe Ectatommini.

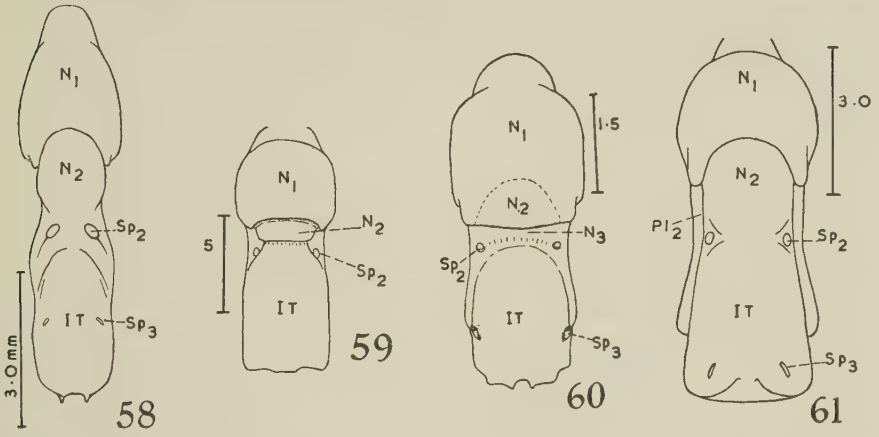
In this tribe the condition of the thorax presents a continuous series from such forms as *Prionopelta punctulata* Mayr and *Typhlomyrmex rogenhoferi* Mayr, where the suture between the pronotum and mesonotum is well marked and the metanotum can be distinguished, to such as the species of *Stictoponera* in which the dorsum is fused into one continuous convex surface and often all but the faintest traces of sutures have been lost. In *Ectatomma tuberculatum* (Oliv.) the suture between the pronotum and mesonotum is much reduced and is merely a narrow line interrupting the sculpturing; the hind margin of the pronotum, as indicated by this suture, is deeply emarginate. The species of *Gnamptogenys* present a good series, commencing with such as *G. concinnum* (Sm.) (fig. 60), in which the suture between the pro- and mesonota is a little fainter than in *Ectatomma tuberculatum*, the hind margin of the pronotum is emarginate, and the metanotum appears as a deep groove. *G. mordax* (Sm.) comes near the middle of the series, it has a much smaller mesonotum than *G. concinnum* and this forms a continuous surface with the pronotum, from which it is separated by a very faint suture which is less curved than that of *G. concinnum*; the metanotum is as before. *G. sulcatum* (Sm.) and *G. tornatum* (Roger) form the end of the series, and in these the dorsum is fused into one convex surface with only the faintest interruption of the sculpturing to indicate the limits of the meso- and metanota. The species of *Gnamptogenys* have a thoracic sculpture that consists of parallel longitudinal grooves; this, in combination with the lack of dorsal sutures in such forms as *G. sulcatum* just described, produces a condition much like that seen in *Cylindromyrmex* (Tribe Cylindromyrmicini).

Tribe Proceratiini.

In this tribe as typified by *Proceratium*, *Sysphincta* and *Problomyrmex*, the dorsum of the thorax is fused into one convex surface with only a very faint trace of the suture between the pro- and mesonota. The metathoracic spiracles are much reduced.

Tribe Ponerini.

There seem to be two types of thorax in this tribe. *Streblognathus aethiopicus* (Sm.) (fig. 61) illustrates one type, in which the pronotum is clearly divided from the mesonotum, but the latter is hardly separated from the metanotum and propodeum and there is very little constriction of the thorax in the region of the metanotum. *Harpegnathos*, *Odontoponera*, *Paltothyreus*, *Neoponera*, *Pachycondyla*, *Bothroponera* and *Plectroctena*, are among the genera which belong to this type; the last mentioned retains the division of the mesopleuron. The second type is typified by *Ponera* itself; the pronotum is distinct from the mesonotum as before, but in addition the metanotum is plainly defined as a furrow and the thorax is somewhat constricted in this region as is normal in other groups. *Brachyponera*, *Trachymesopus* and *Pseudoponera* belong to this type and in these forms the mesopleuron is sometimes divided, and occasionally the suture between the metapleuron and propodeum can be made out.



Figs. 58–61.—Formicidae, 58, *Myrmecia sanguinea*, ☿, dorsal; 59, *Myopopone castanea*, ☿, dorsal; 60, *Gnamptogenys concinnum*, ☿, dorsal; 61, *Streblognathus aethiopicus*, ☿, dorsal.

Tribe Odontomachini.

All parts of the dorsum of the thorax are distinguishable; the pronotum is separated from the mesonotum and the metanotum is groove-like. A characteristic feature of the tribe is the presence of a transverse area delimited anteriorly from the rest of the mesonotum; in *Anochaetus* this area is depressed, in *Odontomachus* it slopes anteriorly, and in *Champsomyrmex* it is raised. There is little doubt that this is a secondary feature of the mesonotum and is not equivalent to any of the primary divisions, as for example the scutum.

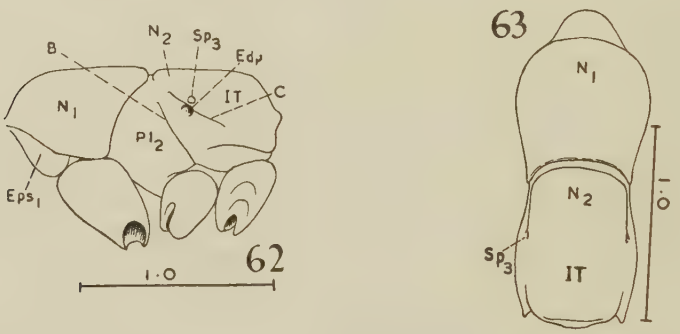
Paraponera clavata (Fab.), tribe Paraponerini, is rather unusual in having the mesonotum depressed instead of convex or flat.

The remaining tribes of the Ponerinae do not call for any special mention. Among the tribes dealt with, the Ponerini, Ectatommini and to a lesser extent the Amblyoponini, are not homogeneous for thoracic type.

Cerapachyinae.

In this subfamily the thorax of the workers is of one type throughout and is characterised by the fusion of all parts of the dorsum into one surface without

sutures, producing an appearance similar to that of the Proceratiini amongst the Ponerines. The pronotal and much reduced metathoracic spiracles usually appear to be about half-way down the pleura; this appearance is particularly marked in such forms as *Phyracaces clarus* Clark, in which there is a strong rim round the dorsum, which has the appearance of marking the junction between the dorsum and pleura, the spiracles being ventral to this rim. Probably the condition is the same as that of *Stigmatomma* (p. 420), where it is suggested that the spiracles, as usual, mark the true line of junction between the dorsum and pleura, the contrary appearance being caused by the abrupt convexity of the dorsum. This explanation would account for the fact that the suture between the pronotum and mesopleuron and that between the meso- and metapleura usually end at the level of the spiracles; there is often a line connecting these two sutures and this probably represents the suture dividing the mesopleuron into two. The metapleural-propodeal suture is sometimes present and meets the meso-metapleural suture at the dorsal termination of the latter. The positions of the pronotal and metathoracic spiracles suggests an affinity with the Amblyoponini, while the fused dorsum makes one suspect a connection with the Proceratiini.



Figs. 62–63.—Formicidae, *Dorylus helvolus*, 62, ☿, lateral; 63, ☿, dorsal.

Dorylinae.

There are two distinct types of worker thorax in this subfamily; one is typical of the tribe Dorylini, the other of the Ecitonini; Tulloch described only the former type.

Tribe Dorylini.

Dorsally the thorax of the workers and soldiers is composed of two parts of about equal size, the anterior part is the pronotum and the posterior part is composed of the mesonotum, metanotum and propodeum. In *Dorylus helvolus* (L.) (figs. 62 and 63), an anterior region of the mesonotum is depressed below the rest and at first this narrow region may be mistaken for the whole of the mesonotum, but careful examination will sometimes reveal faint signs of the true line of junction between the mesonotum and metanotum plus propodeum, and comparison with other forms and with the queen confirms this. This depressed region of the mesonotum is not developed in all the subgenera of *Dorylus*. Laterally the thorax of *D. helvolus* is somewhat distinctive (fig. 62). The meso-metapleural and metapleural-propodeal sutures are incomplete but

deeply impressed; the latter is just ventral to the large propodeal spiracle and passes through the large endophragmal pit. There is a groove which passes anteriorly, arising from the opening of the metapleural gland; at first it may be mistaken for a part of the metapleural-propodeal suture. The thorax of the queens of the Dorylini is of the same type, but is in an earlier stage of reduction; the sutures on the pleura are complete and better marked and the sutures limiting the meso- and metanota are faintly visible.

Tribe Ecitonini.

The thorax is a single whole and the sutures are more reduced in some of these forms than in any other ants. The thorax of *Eciton* (*Acamatus*) *pilosum* Sm. (fig. 64) lacks even the pleural sutures, but the pronotal, mesonotal and propodeal regions can be identified by differences of contour. The endophragmal pit is conspicuous and occupies much the same position with respect to the propodeal spiracle as that of *Dorylus helvolus*. In *Cheliomyrmex nortoni* Mayr the dorsum of the thorax is much flatter than in *Eciton pilosum*, so that the notal areas are less easy to identify, with the exception of the metanotum which is groove-like. In *Eciton* (*Labidus*) *crassicorne* Sm., the posterior margin of the mesonotum overhangs the metanotal depression, so that at first it

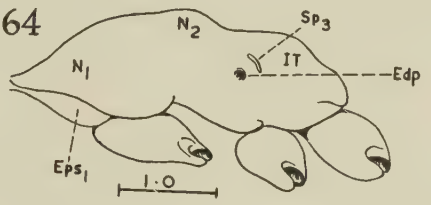


Fig. 64.—Formicidae, *Eciton pilosum*, ☿, lateral.

looks like the posterior margin of the pronotum. In the subgenus *Eciton* the condition is much like that of *Cheliomyrmex* but the metanotum is less distinct.

Aenictus has a thorax much like that of the subgenus *Eciton*.

Tribe Leptanillini.

Wheeler (1928) suggested that the genus *Leptanilla*, the sole member of the tribe, should be placed in a separate subfamily. So far as the worker thorax is concerned, it is of the *Dorylus* type, being divided dorsally into two equal parts, and in general appearance it is similar to that of *Dorylus*.

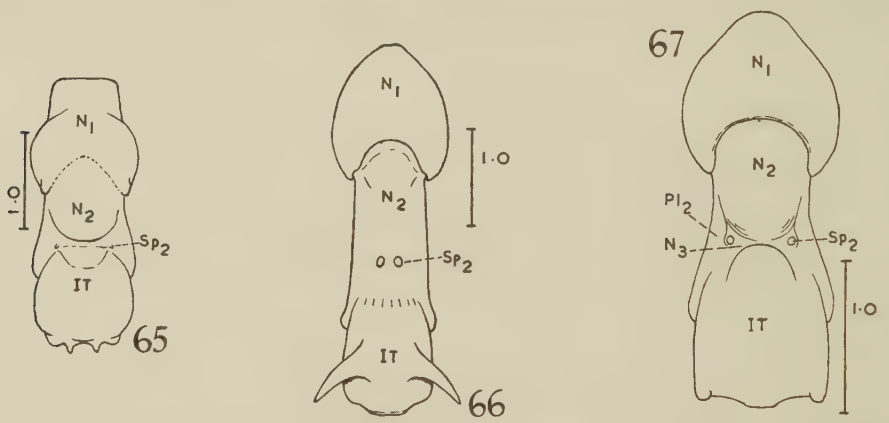
Except for *Aenictus* and *Leptanilla* the Doryline thorax seems to be characterised by the large endophragmal pit which is placed just anterior or anteroventral to the propodeal spiracle.

Pseudomyrminae.

The thorax of the workers is relatively unspecialised, the suture between the pronotum and mesonotum is well developed and the mesonotum is separated from the propodeum by the groove-like metanotum. In *Tetraponera* the metathoracic spiracles are close together, indicating that the dorsum in this region is narrow. The meso-metapleural suture is deeply impressed. *Pseudomyrma* is similar except that the spiracles are not closer together than normal and the meso-metapleural suture is not deeply impressed.

Myrmicinae.

Throughout this large group the thorax is essentially of one type. The suture between the pronotum and mesonotum is always much reduced, sometimes entirely obliterated, and the other sutures both pleural and dorsal are much reduced, but the parts of the thorax can nearly always be identified by their differences of contour. Typically the pronotum is the widest part of the thorax and the metanotum, which is depressed, is the narrowest. *Manica* (fig. 65) has the sutures fairly well developed, the mesopleuron is divided and the metapleural-propodeal suture is visible. *Messor* has a very large pronotum, relatively larger than that of the winged females. In this genus and in *Aphaenogaster*, as well as others, the thorax has a rather characteristic appearance when viewed from the side. The pronotum is at a much higher level than the propodeum and the mesonotum slopes steeply so as to connect the two. This raising of the pronotum appears to have the effect of providing enough room to accommodate the enlarged fore coxae, with which the enlargement of the pronotum is no doubt correlated. The metanotum of *Myrmicaria* appears



Figs. 65–67.—Formicidae, 65, *Manica rubida*, ☿, dorsal; 66, *Dolichoderus decollatus*, ☿, dorsal; 67, *Formica exsectoides*, ☿, dorsal.

as a sharp declivity posterior to the mesonotum. Certain species of *Crematogaster*, *e.g. C.* (*Physocrema*) *inflata* Sm., have a much enlarged propodeum; otherwise the thorax is normal. In *Myrmecina* and *Pristomyrmex* the dorsum is without projecting or depressed areas and is almost one surface. This condition leads to that seen in *Cryptocerus* and allied genera where the dorsum is largely at one level, and is almost sutureless with a projecting rim all round. In these forms the suture between the pronotum and mesopleuron and that between the mesopleuron and metapleuron are well developed. The thoraces of *Melissotarsus* and *Rhopalomastix* (Tribe Melissotarsini) are not at all like the typical Myrmicine thorax, for the dorsum is without sutures and presents a single convex surface, rectangular when viewed from above. The thorax of these forms is more like that of such a Ponerine as *Proceratium* than like that of any Myrmicine, and in the past they have been placed among the Ponerinae.

Dolichoderinae.

The thorax is of the generalised type seen in *Myrmecia*. There is a well-formed suture between the pro- and mesonota, and the metanotum is a de-

pressed area not usually bounded by sutures (fig. 66, *Dolichoderus decollatus* Sm.). Sometimes the metathoracic spiracles are very close together, indicating that the dorsum in this region is very narrow. This is well illustrated by *Dolichoderus attelaboides* (Fab.), for in addition to the closeness of the spiracles, lines indicating the junction between the mesonotum and mesopleura are present and the position of these shows that the mesonotum is very narrow. This narrowing of the mesonotum is a frequent occurrence in forms with long and slender thoraces, and *Dorymyrmex planidens* Mayr is a further example.

Formicinae.

(Fig. 67, *Formica exsectoides* For.)

I have not discovered any constant difference between the thorax of this subfamily and that of the Dolichoderinae and in essentials it is just the same; the pronotal suture well developed and the meso- and metanota distinguishable. There is a tendency for the propodeum of the Dolichoderinae to be more prominent than that of the Formicinae, while in the Formicinae the thorax of *Camponotus*, and other genera like it, has a rather characteristic "facies." The mesonotum, metanotum, and propodeum are all at about the same level, thus tending to form an uninterrupted dorsal surface which is rather narrow; there is a faint but definite suture between the meso- and metanota and sometimes a fainter one between the metanotum and propodeum.

Conclusions.

The impression one gains from a study of the thorax of worker ants is that there is too much continuous variation, and not enough discontinuous, to enable one to draw many detailed conclusions bearing upon classification. However, a few observations may be made. Briefly Wheeler's views on the relations of the subfamilies (Wheeler, 1928) are as follows. He considered the Ponerinae to be the primitive group from which the other subfamilies have diverged. The Cerapachyinae and Dorylinae form one branch and are the next most primitive groups, the former being supposed to connect the Dorylinae to the Ponerinae. The Pseudomyrminae and Myrmicinae form a second branch and the Formicinae and Dolichoderinae a third.

In thoracic characters the Ponerinae display by far the greatest diversity, which is perhaps in keeping with the view that they are the oldest group and have therefore had a longer time in which to differentiate. All types of thorax encountered in the other subfamilies have a counterpart amongst the Ponerinae, and such forms as *Myrmecia* are considered to be among the most primitive of living ants. On this point the evidence of the worker thorax appears to be negative or even contradictory; the thorax of workers of *Myrmecia* does not appear to be any more primitive than that of *Dolichoderus*, for instance, while the thorax of such as *Proceratium* is very specialised. It is evidently not possible to say from a study of the worker thorax which group of ants is the most primitive and which the most highly developed, nor is it possible to find much evidence for or against the views generally held on this subject, but this question will be alluded to later.

The thorax of the Cerapachyinae is of a uniform type and seems to have affinities with the thorax of certain of the tribes of the Ponerinae (p. 422). The condition of the worker thorax does not support the view that this subfamily is intermediate between the Ponerinae and Dorylinae, for the thorax of *Dorylus* is less specialised than that of the Cerapachyinae. The thorax

of the Dorylinae is of two distinct types, bipartite in the tribe Dorylini and Leptanillini and usually undivided by any sutures in the Ecitonini. In the remaining four subfamilies the thorax of the workers is of one type throughout each. The thoraces of the Dolichoderinae and Formicinae are very similar. The thorax of the Myrmicinae is somewhat distinctive, though in a general way similar to that of the Pseudomyrminae. Certain species of *Ectatomma* (Ponerinae) have a thorax which is rather similar in appearance to that of a typical Myrmicine. The thorax of *Camponotus* (Formicinae) is rather like that of such Ponerine genera as *Streblognathus* and *Odontoponera*.

Tulloch (1935) found that a study of the thorax based largely on that of the winged females supported Wheeler's arrangement of the subfamilies. He found very little similarity between the thoraces of the Cerapachyinae and Dorylinae and in this respect my conclusions agree with his. He found that the alate thorax of the Myrmicinae is easily recognised; the same is true of the worker thorax. He stated that the Myrmicinae display considerable diversity; rather the reverse is true of the worker thorax except superficially. He found that the thoraces of the Dolichoderinae and Formicinae are very similar and this is true of the worker thorax.

It has already been remarked (p. 425) that the worker thorax is not helpful in deciding which group is the most primitive and *vice versa*; on the contrary one is struck by the fact that the worker thorax of the Formicinae, which is considered to be the most highly developed group, is more generalised than that of many Ponerinae. However, it is probably justifiable to maintain that the specialised forms of thorax found among the Ponerinae display degenerate specialisation. Further, the classification of the ants is based on habits as well as on structure.

Tulloch has studied the thorax of forms intermediate between the females and the workers in *Pogonomyrmex californicus* (1930) and *Monomorium rubriceps* (1930a). These investigations show clearly that what I have inferred from series of species in other families is correct, namely that the first part of the thorax to undergo modification and reduction when the wings are reduced is the mesonotum, and that it undergoes greater reduction in size than other parts of the thorax. Tulloch's investigations show further that the loss of all secondary divisions on the mesonotum takes place rapidly in ants and is not preceded by any great increase in size of one part at the expense of another, as occurs in the Thynnidae, Tiphiidae, and Bethylidae. The process of modification in these two genera of ants seems to take place roughly in the following order :—

1. Great reduction in size and simplification of the mesonotum.
2. Metanotum and metapleura fuse.
3. Fusion of the metapleuron with the propodeum if they were separate originally. Disappearance of the sutures between the mesonotum, metanotum and propodeum.
4. Loss of the division of the mesopleuron.
5. Fusion of the pronotum and mesonotum.

No. 5 occurs because *Pogonomyrmex* and *Monomorium* are Myrmicine genera. Tulloch noted that the relative size of the pronotum increases. This is most obvious among ants in the Myrmicinae and I have drawn attention to it in *Messor* (p. 424).

The wide diversity of type among the thorax of worker ants makes it difficult to say what type of wingless thorax is most characteristic of the

Formicidae. In these circumstances it seems best to choose a generalised type of thorax from which the specialised ones seem to be derived, such, for example, as that of the species of *Myrmecia* (fig. 58). Then the following is a description of the type of wingless thorax apparently most characteristic of the Formicidae. Essentially the thorax is composed of two parts, the pronotum and the remainder. The pronotum is separated from the mesonotum and mesopleura by a well-marked suture; it is somewhat globose and is the widest part of the thorax. The mesonotum is convex and is considerably smaller than the dorsal surface of the pronotum and is without any secondary divisions; it is separated from the mesopleura by sutures but is usually continuous with the metanotum, which is in turn continuous with the propodeum. The metanotum is also fused with the metapleural regions and is only recognisable because of being depressed below the level of the mesonotum and propodeum; it is a transverse area, shortest medially and expanding on either side to form areas in which the metathoracic spiracles are situated. The propodeum, including the metapleura, is about equal in size to the pronotum; the propodeal spiracles are large. The mesopleura are separated by sutures, anteriorly from the pronotum and posteriorly from the metapleura; they are without epimera and are undivided; viewed from above they do not project strongly on either side of the dorsum. The metapleura are fused dorsally with the metanotum and posteriorly with the propodeum; the metapleural glands open upon them postero-ventrally.

It is generally agreed (Wheeler, 1928) that the ants have sprung from some Scolioid or Bethyloid form or some form ancestral to these. The type of thorax just described is not particularly like any of the types of wingless thorax already described among the Scolioids and Bethyloids.

Material examined (one or more species have been examined in the following genera) :—

Ponerinae.—*Myrmecia, Pristomyrmecia, Myopopone, Amblyopone, Stigmatomma, Platythyrea, Prionopelta, Typhlomyrmex, Ectatomma, Chalcoponera, Holcoponera, Gnamptogenys, Stictoponera, Proceratium, Sysphincta, Problomyrmex, Paraponera, Harpegnathos, Odontoponera, Streblognathus, Paltothyreus, Neoponera, Pachycondyla, Bothroponera, Trachymesopus, Eubothroponera, Plectroctena, Brachyponera, Pseudoponera, Ponera, Onychomyrmex, Leptogenys, Lobopelta, Anochaetus, Odontomachus, Champsomyrmex.*

Cerapachyinae.—*Cerapachys, Parasyscia, Phyracaces, Lioponera, Sphinctomyrmex.*

Dorylinae.—*Dorylus* (with subgenera *Dorylus, Anomma, Typhlopone, Dichthadia*), *Eciton* (with subgenera *Eciton, Acamatus, Labidus*), *Cheliomyrmex, Aenictus, Leptanilla.*

Pseudomyrminae.—*Tetraponera, Pseudomyrma.*

Myrmicinae.—*Myrmica, Manica, Pogonomyrmex, Messor, Aphaenogaster, Pheidole, Melissotarsus, Rhopalomastix, Stereomyrmex, Myrmicaria, Cardiocondyla, Crematogaster, Monomorium, Solenopsis, Myrmecina, Pristomyrmex, Dacryon, Meranoplus, Leptothorax, Microthorax, Formicoxenus, Harpagoxenus, Ocymyrmex, Tetramorium, Cataulacus, Cephalotes, Cryptocerus, Daceton, Atta, Proatta, Apterostigma.*

Dolichoderinae.—*Dolichoderus, Hypoclinea, Leptomyrmex, Iridomyrmex, Azteca, Dorymyrmex, Engramma, Tapinoma, Technomyrmex, Semonius.*

Formicinae.—*Melophorus, Notoncus, Lasiophanes, Myrmelachista, Decamera, Acantholepis, Plagiolepis, Myrmoteras, Myrmecorhynchus, Brachy-*

myrmex, Gigantiops, Opisthopis, Camponotus, Myrmopsamma, Oecophylla, Polyrhachis, Acanthomyops.

17. Proctotrupoidea.

On the whole the thorax of the wingless forms in this superfamily is not highly modified. The figures and descriptions of certain species given by Kieffer (1914 : 16 and 26) suggest that these have very peculiar thoraces, but in most instances the figures are not to be relied upon; for example, in a number of figures of winged forms, the hind-wings are represented as attached to the mesoscutellum or to the propodeum. Nevertheless a small proportion of these wingless forms described by Kieffer undoubtedly have highly modified thoraces, more specialised than any I have seen. There is a marked tendency for each family to have a thoracic type peculiar to itself and in the wingless forms of each family the type tends to be accentuated.

The thorax of the wingless forms in the families Proctotrupidae (Serphidae) and Diapriidae is similar. Fig. 68 shows a dorsal view of the female thorax of *Platymischus dilatatus* Westw. (Diapriidae). Wings are absent and the mesonotum has become quite flat, but the scutum and scutellum are still

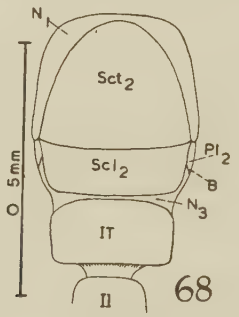
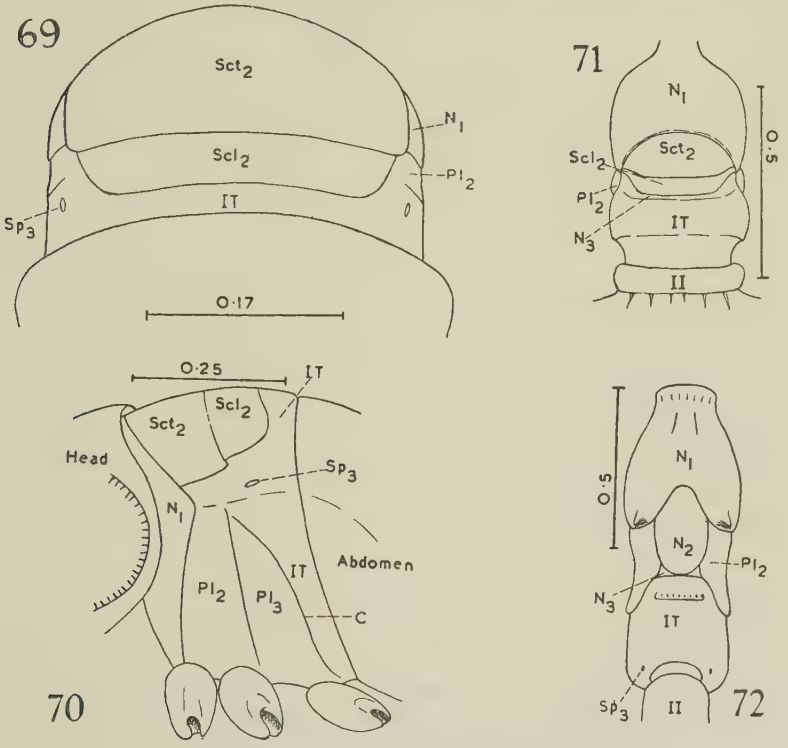


Fig. 68.—*Platymischus dilatatus* (Proctotrupidae), ♀, dorsal.

large and the pronotum occupies the same position and is of much the same shape and size as in the winged forms; there is none of the growth posteriorly of the pronotum which has been characteristic of many of the families dealt with so far. The metanotum is a transverse groove. Other genera of Diapriidae containing wingless forms are *Zacranium*, *Platymischoides*, *Solenopsia*, *Eriopria* and *Mantara*; all of these have the same type of thorax as *Platymischus dilatatus*, but some are more modified and the mesonotum has become narrower, causing the scutum to become elongate oval in shape, while more of the pronotum is visible from above. *Paracodrus apterogynus* (Hal.) is an example of a wingless form among the Proctotrupidae.

In the Scelionidae there is the same tendency for the pronotum to remain unchanged in shape and size in the wingless forms; but the thorax is short and broad while that of the Proctotrupidae and Diapriidae is long and slender and in the wingless forms becomes more slender. Similarly the thorax in the wingless Scelionidae tends to become shorter and broader than that of the winged forms. Figs. 69 and 70 show dorsal and lateral views of the female thorax of *Baeus curvatus* Kieff. (Scelionidae, Baeini). This is a most curious little insect in which the abdomen fits closely against the back of the propodeum so that it is difficult to be certain of their limits. This character is probably an accentuation of the condition seen in many Proctotrupids in which a

process on the petiole fits into an excavation in the back of the propodeum and the anterior face of the second abdominal segment; possibly in *Baeus* the petiolar segment is entirely enclosed between the propodeum and second abdominal segment. The scutum and scutellum of *B. curvatus* are well developed though much flattened, the pronotum is invisible from above except for a small area laterally. The metanotum is not distinguishable and is perhaps fused with the propodeum. The thorax of *Parabaeus ruficornis* Kieff. does not conform to the type of wingless thorax characteristic of the SCELIONIDAE. The pronotum has a dorsal surface and all of the thorax posterior to the pro-



FIGS. 69–72.—69–70, *Baeus curvatus* (SCELIONIDAE), 69, ♀, dorsal; 70, ♀, lateral; 71, *Lagynodes pallidus* (CALLICERATIDAE), ♀, dorsal; 72, *Betyla fulva* (BELYTIDAE), ♀, dorsal.

notum is fused together and devoid of sutures. For a figure of this species see Kieffer (1926 : 133).

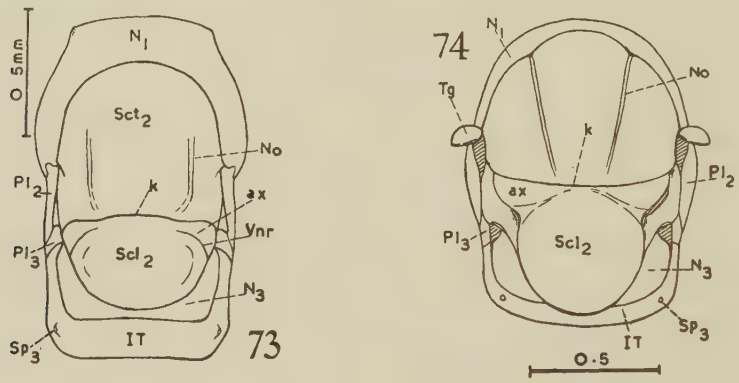
In the CALLICERATIDAE, unlike the three families just dealt with, the pronotum becomes enlarged and produced backwards, and the mesonotum is reduced in size accordingly. Fig. 71 shows the dorsal aspect of the female thorax of *Lagynodes pallidus* (Boh.) which exemplifies the Calliceratid type of wingless thorax. The metanotum is almost fused with the propodeum. *Plastomicrops acuticornis* Kieff. (Kieffer, 1914 : 130) evidently has a thorax of the same type as that of *Lagynodes pallidus* but the modification has gone much further, for the pronotum extends far back and the mesonotum has become very small; Kieffer describes the pronotum as occupying most of the thorax. *Pristomicrops clavatus* Kieff. (*loc. cit.* : 126) is evidently much the same.

The thorax of *Betyla fulva* Cam. (fig. 72) (Belytidae) is somewhat intermediate in character between that of the Diapriidae and Calliceratidae. The pronotum is somewhat backwardly produced as in the Calliceratidae, but the hind margin is narrowly emarginate, so that the scutellum is elongate oval as in the Diapriidae. The scutum and scutellum have fused; what appears to be the metanotum is small and fused with the scutellum.

18. Cynipidae.

Although wingless forms are quite common in the Cynipidae and some of these have the thorax much reduced in size, there is extremely little modification, and the relation of the sclerites to one another is much the same as in the winged forms.

Figs. 73 and 74 show dorsal views of the female thorax of the agamic and sexual forms of *Biorrhiza pallida* (Oliv.). Comparison of the thorax of the agamic form (form *aptera* Bosc) with the winged thorax of the sexual form



Figs. 73–74.—*Biorrhiza pallida*, 73, (form *ptera*) (Cynipidae), ♀, dorsal; 74, (sexual form), ♀, dorsal.

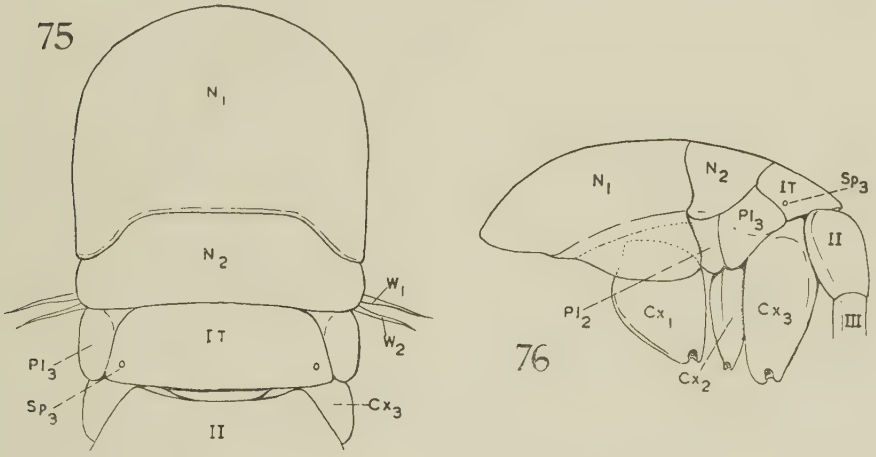
shows that there has been reduction in size and simplification of the mesonotum, but little else. In side view the mesonotum of the agamic form is much less convex than that of the winged form; it is also shorter so that in dorsal view more of the pronotum is visible and the median section of the metanotum is not hidden, as it is in the sexual form, by the projecting posterior end of the scutellum.

The female thorax of *Trigonaspis megaptera* form *renum* (Hartig) is essentially similar to that of the agamic form of *Biorrhiza pallida*. Certain other wingless forms among the Cynipinae have the scutellum knoblike, for example *Zopheroteras sphaerula* Weld. Among the Charipinae, species of *Nephycta* and *Pezophycta* have the wings very abbreviated, but the thorax is almost unmodified.

19. Chalcidoidea.

Except for the curious fig insects, the thorax of the wingless Chalcids displays very little simplification or fusion; consequently this section will be devoted largely to a discussion of the thorax of the male fig insects (Agaonidae and Torymidae, Idarninae), which in many genera is very difficult to interpret.

Contrary to the normal state of affairs, it is the males and not the females which are wingless in the fig insects; they are morphologically extremely aberrant and this applies to the thorax as much as to the rest of the body. From 1916 onwards Grandi has published many papers on the fig insects and these contain numerous figures. He has investigated the morphology of a number of species, but so far as the thorax of the males is concerned his interpretations of the notal regions do not appear to be always consistent, because he has not homologised certain sclerites among the various genera. Figs. 75 and 76 are dorsal and lateral views of the thorax of the male of *Philotrypesis caricae* (L.), Torymidae; it appears to me that by a study of this thorax it is possible to interpret the structure of the more aberrant thoraces in a consistent manner. The dorsum forms a single convex surface, the pronotum is considerably enlarged and has a pair of lateral extensions which cover the bases of the first pair of coxae; the mesonotum is devoid of any secondary divisions

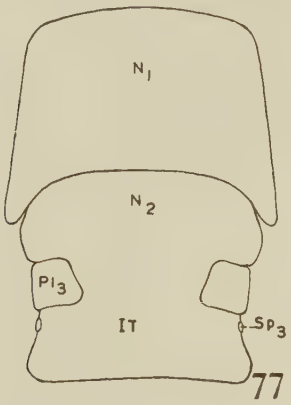


Figs. 75–76.—*Philotrypesis caricae* (Torymidae), 75, ♂, dorsal; 76, ♂, lateral.

and the propodeum is identifiable by the large propodeal spiracles. A more special feature of this thorax is a sclerite seen in dorsal view on either side of the propodeum. Grandi (1921) calls these sclerites the metanotum, but for a number of reasons it appears to me that they are the metapleura; they certainly do not look like the metanotum. In the lateral view (fig. 76) it will be seen that this dorsal sclerite is continuous with what is undoubtedly the metapleuron and if the figure is compared with figs. 44, 45, and 48 in Snodgrass (1910) it will be seen that the whole structure occupies a position with respect to the propodeum that is the normal position for the metapleuron in many Chalcids. Furthermore the figures of Snodgrass show that the metanotum is anterior to the metapleuron and it seems to me that the true metanotum of *Philotrypesis* is in the same position but has fused with the mesonotum; the position of the hind-wing (fig. 75) supports this idea, for it is anterior to this sclerite that Grandi calls the metanotum, but is level with the posterior border of the mesonotal sclerite, which I suggest is the metanotum. The only objection to supposing that this sclerite is the metapleuron is its large dorsal surface, but this is readily explained by the extremely large posterior coxae which have no doubt necessitated an increase in the size of the metapleura; the same effect

has already been seen in the THYNNIDAE, TIPHIIDAE and BETHYLIDAE, where the legs of the females are very powerful and the mesopleura of some forms develop a dorsal surface.

Assuming that the suggested explanation of the thoracic structure of *Philotrypesis caricae* is correct, one may attempt to explain the thoracic structure of the more aberrant forms on the same basis. Fig. 77 is a dorsal



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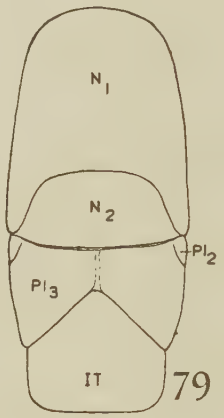

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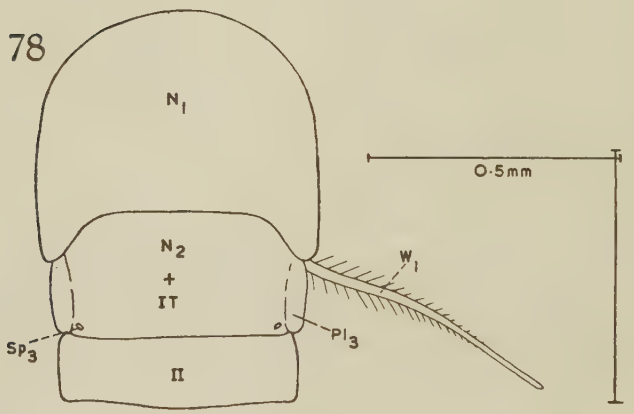


FIGS. 77–79.—77, *Blastophaga psenes* (AGAONIDAE), ♂, dorsal; 78, *Eupristina masoni* (AGAONIDAE), ♂, dorsal; 79, *Kradibia cowani* (AGAONIDAE), ♂, dorsal.

aspect of the male thorax of *Blastophaga psenes* (L.) (AGAONIDAE); comparison with that of *P. caricae* shows that the suture between the mesonotum (plus metanotum) and the propodeum has been lost, while the relative positions of the metapleura and propodeum have changed. Grandi (1920) is noncommittal and called the dorsal surfaces of the metapleura "latero-dorsal areas of the metathorax." Fig. 78 shows the dorsal thoracic aspect of *Eupristina masoni* Saund. (AGAONIDAE). The mesonotum, metanotum and propodeum are fused as in *B. psenes* and the sutures between the propodeum and metapleura are partially obliterated. Fig. 79 shows the dorsal thoracic aspect of *Kradibia*

cowani Saund. (AGAONIDAE). This form and others like it are the most difficult to interpret. Following the explanation adopted so far, the large area between the mesonotum and propodeum is composed of the metapleura, which from either side have grown towards the median dorsal line until they have met and fused, thus separating the mesonotum (plus metanotum) from the propodeum. This, if true, is an extraordinary thing to have occurred, but this explanation is consistent with the condition in *Philotrypesis caricae* and *Blastophaga psenes*; moreover there is a faint median dorsal line which can readily be explained as the line of fusion of the two metapleura but is difficult to explain otherwise. *Ceratosolen gravelyi* Grandi (Grandi, 1917 : fig. 11) seems to show a condition that is much like that of *Kradibia cowani* but a little less advanced; the propodeum is prolonged anteriorly as a narrow median tongue-like process which meets the mesonotum (plus metanotum) and on either side of which lie the two large metapleural sclerites like those of *K. cowani*; Grandi calls these the metanotum.

Since the structures I have been considering are metathoracic they must be either metapleura or metanotum; either alternative involves difficulties and there is no escaping the conclusion that the thorax of some of these forms is highly aberrant, but it appears to me more reasonable to consider these sclerites to be the metapleura than the metanotum. If one supposes that these sclerites are metanotal one has to face the following difficulty. The thorax of *Philotrypesis caricae* is plainly less specialised than that of *Kradibia cowani* and similar forms, yet there seems no doubt that in *P. caricae* the dorso-lateral sclerites are entirely or almost entirely parts of the metapleura, while the metanotum is much reduced as is normal in very modified wingless Hymenoptera. But the supposed metanotum of *Kradibia*, *Ceratosolen* and others is enormously larger than that of *P. caricae*, and to explain this one must suppose that the metanotum, having become much reduced in the forms antecedent to *Kradibia* which were presumably much like *Philotrypesis*, then became enlarged again until it attained a quite abnormal shape and size. Such a hypothesis runs counter to the evolutionary rule that structures once lost (or reduced) are not regained. It is evident that to settle the homologies of the parts of the thorax in the males of the AGAONIDAE and TORYMIDAE, a re-investigation of the problem will be necessary.

Besides the more aberrant forms already discussed, there is a number of species of fig insects in which the dorsum of the male is more normal, being composed of three areas often of about equal size; the pronotum, mesonotum and propodeum. These three areas are separated by sutures, they are usually more or less rectangular, and as in the genera discussed so far they form one smooth convex surface. Such forms are found in the genera *Liporrhopalum*, *Sycophaga*, *Ganosoma* and *Pleistodontes* among the AGAONIDAE; the last-mentioned genus has a thorax which appears to be similar to that of *Eupristina*. Among the TORYMIDAE are the genera *Sycoscapter* and *Sycobiella*, in which the propodeum is very transverse and therefore of smaller area than the pro- or mesonota.

Among the rest of the Chalcidoidea, I know of short-winged or wingless forms among the following families :—1. EULOPHIDAE, 2. ENCYRTIDAE, 3. EUPELMIDAE, 4. CLEONYMIDAE, 5. PTEROMALIDAE, 6. EURYTOMIDAE, 7. MISCOGASTERIDAE, 8. TRICHOGRAMMATIDAE. I have seen short-winged or wingless forms from all except no. 6; none of these forms displays much fusion or simplification of parts. Among the EUPELMIDAE considerable changes occur in the shape of the thoracic sclerites in the flightless forms, but these

changes result only in an intensification of the features characteristic of the winged forms. The thorax of the EUPELMIDAE is somewhat peculiar and is well illustrated by Snodgrass (1910 : figs. 40 and 41, *Cerambycobius cushmani* Crawf.). In the flightless forms the pronotum becomes rather more distinct from the rest of the thorax; the scutum and scutellum continue to be very independent of one another and both become considerably narrower, while the longitudinal ridges upon them become much accentuated. This is particularly true of the lateral longitudinal ridges of the scutum which appear to correspond to parapsidal furrows; these become very prominent in the wingless forms and tend to overhang the parapsides. The notaulices become fainter and the part of the scutum enclosed between the parapsidal ridges tends to become concave. As the scutellum becomes narrower the sutures separating the notal axillae from the scutellum (the true scuto-scutellar suture, see p. 371) become more nearly longitudinal; this is well seen in *Eupelmus epicaste* Walk., in which the scutellum is little more than a longitudinal carina. In all the species I have seen, the wings are present though they may be much reduced, they are directed backwards and applied closely to the areas of the thorax separating the mesopleura from the scutellum; terminally they are abruptly turned upwards in a characteristic manner.

In the TRICHOGRAMMATIDAE, Salt (1937) has recorded a most interesting and exceptional case of wing reduction in *Trichogramma semblidis* (Auriv.). When this Chalcid is bred from the eggs of the alder fly *Sialis lutaria*, the male parasites which emerge are almost all wingless, or to be exact have the wings reduced to minute lobes; but when reared in the eggs of moths such as *Ephestia* the males are always fully winged. In addition to the presence or absence of wings, there are other differences between the two forms; the antennae are different and the legs of the flightless forms are stouter than those of the fully winged. Very small changes have occurred in the thorax externally beyond the usual reduction in size; this allows the pronotum to be partially visible dorsally while it is concealed by the scutum in the fully winged form. But as Salt points out, the winged males and females have an enormous postphragma extending back into the abdomen, and this appears to be entirely missing in the flightless males.

Material examined :—

PTEROMALIDAE.—*Tricoryphus fasciatus* Thoms., *Dipara cupreiceps* (Walk.), *Theocolax formiciformis* Westw.

EUPELMIDAE.—*Eupelmus testaceus* Cam., *brevipennis* Cam., *Eupelminus excavatus* (Dalm.), *tarsatus* Watst., *Eupelmella mullneri* Ruschka, *Anastatus antestiae* Ferr., *ameleophagus* Bern.

ENCYRTIDAE.—*Dinocarsis hemiptera* (Dalm.), *Ectroma maderense* Walk., *rufum* (Dalm.), *Pezobius insignis* Mercet, *Metanotalia hispanica* Merc., *Beocharis pascuorum* Mayr, *Anusia fulvescens* (Westw.), *Choreia inepta* (Dalm.), *Metallon atriceps* Walk.

EULOPHIDAE.—*Closterocerus africanus* Watst.

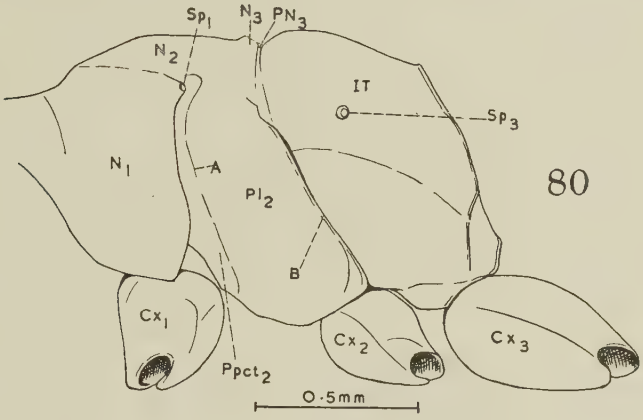
MISCOGASTERIDAE. Certain LELAPINAE.

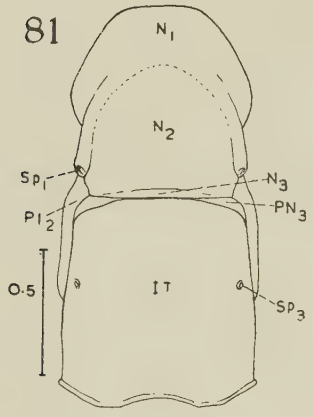
20. Ichneumonoidea.

Wingless forms occur among the ICHNEUMONIDAE, subfamily CRYPTINAE, and among the BRACONIDAE; of these wingless forms only certain of the Cryptine Ichneumonids are much modified.

(i) Ichneumonidae.

Figs. 80 and 81 show lateral and dorsal aspects of the female thorax of *Gelis* (= *Pezomachus*) *palpator* (Grav.). In effect the female thorax is composed of two parts: the pro- and mesonota and the metanotum form the anterior part, while the propodeum forms the posterior. The mesonotum has been much reduced in size and the scutum and scutellum are indistinguishably fused. The pronotum has been only slightly altered in size and shape and has





Figs. 80–81.—*Gelis palpator* (Ichneumonidae), 80, ♀, lateral; 81, ♀, dorsal.

fused with the mesonotum, so that the line of the suture is only faintly visible. The metapostnotum forms a deep transverse groove between the metanotum and propodeum; the latter has increased in relative size and some of this increase has taken place anterior to the spiracle. Laterally the prepectus of the mesopleuron is a little more clearly defined than in the male; the division of the mesopleuron has been lost and the epimeron is not as well defined. The dorsal part of the metapleuron which is continuous with the metapostnotum has become much smaller.

The females of other species of *Gelis* only differ very slightly from the condition just described; in some species reduction has not gone quite so far

so that the dorsal pronotal suture is more clearly visible and the scutellum can be faintly distinguished from the scutum; e.g., *G. vagans* (Grav.). A few species are a little more highly modified than *G. palpator* and in these the dorsal pronotal suture is quite lost and the metanotum cannot be made out. The female of *G. hieracii* (Bridgm.) is somewhat different in appearance from the majority of the species; the thorax is long and slender and black, the pronotal suture is well defined and the metanotum is large and clearly divided from the mesonotum and propodeum. *G. albicinctus* (Ruthe) female is somewhat intermediate between *G. hieracii* and the normal type.

Amongst other genera of Cryptine Ichneumonids all conditions of the thorax exist, from the highly modified type described in *G. palpator* to the unmodified fully winged thorax. Some intermediate forms are *Hemiteles subzonatus* (Grav.), *H. pedestris* (Fab.), and *Microcryptus nigrocinctus* (Grav.).

Material examined :—*Pezoporus brachypterus* (Grav.), *Hemiteles atricapillus* (Grav.), *pedestris* (Fab.), *hemipterus* (Fab.), *Phygadeuon gravenhorsti* Först., *procerus* Grav., *Gelis micrurus* (Först.), *intermedius* (Först.), *blandus* (Först.), *vagans* (Grav.), *cursitans* (Grav.), *instabilis* (Först.), *fasciatus* (Fab.), *zonatus* (Först.), *canaliculatus* (Först.), *gentilis* (Först.), *tener* (Först.), *transfuga* (Först.), *Cremnodes nanodes* Först., *Otacustes caffer* Turn.

(ii) Braconidae.

There are not very many flightless Braconids and the majority of these retain at least stumps of the wings, consequently it is not surprising to find that there appear to be no species with highly modified thoraces. *Spathius apterus* Woll., and *S. apotanus* Wilkn., are the most modified I have seen; in these two species there has been no fusion of the parts, but the mesonotum is considerably reduced in size and the scutellum has become knoblike, while the metapostnotum is moderately deeply depressed. The tendency of modification in these two species appears to be towards the type of thorax displayed by *Gelis*. *Ecphylopsis nigra* Ashm. has a strongly knobbed scutellum and *Chasmodon apterus* (Nees) also has the scutellum somewhat knobbed. Possibly this formation of the scutellum is characteristic of the flightless Braconids, but something similar can be seen in certain of the less highly modified flightless Cryptinae.

(iii) Myersiidae.

The female of *Thaumatotypus billupsi* Bridgm. has a much-modified thorax, but it is closely similar to that of the females of *Gelis*.

(iv) Megalyridae.

The female of *Megalyra mutilis* Westw. has the wings reduced to about half the normal length, but, as might be expected with such comparatively slight reduction, the thorax shows no obvious differences from that of the fully winged forms.

VII. *The numbers of flightless species in the various groups of Hymenoptera.*

In the following tables data are given of the numbers of flightless forms occurring in the different groups of Hymenoptera; these data are necessarily more or less approximate. Except in those groups where it is stated that indirect means have been employed to calculate the numbers of flightless species, the data have been taken mostly from works dealing with the respective groups and the small figures against the group names in the tables refer to the

footnote in which brief references to these works are given; for the full references see the list of references at the end of this paper. Where the monographic literature to a group is not recent the figures have been brought up to date by consulting the *Zoological Record*. In those groups in which indirect means were used to calculate the numbers of flightless species, the method was to determine the proportion of flightless to normal forms in the material of the group in the British Museum; knowing the total numbers of species in the groups a rough estimate of the numbers of flightless species could then be made.

Groups in which all the species have one or both sexes flightless.

Group	Number of species	Number of genera
Mutillidae [1]	3500–4000	100
Myrmosa [2]	22	2
Chyphotes [2]	10	1
Apterogynidae [2]	44	2
Bradynoboenus	2	1
Typhoctes [2]	2	1
Methoca [2]	41	1
Thynnidae [3]	480	50
Formicidae	3500	200
Embolemidae	8	2
Sclerogibbidae	10	2
Agaonidae [4]	130	18

Groups with less than 100% of the species flightless.

Group	Total no. of spp.	Total no. of gen.	No. of spp. flightless	No. of gen. having flightless spp.	Percentage of spp. flightless
Bethylidae [5]	650	100	150	30	23
Dryinidae [5]	400	50	200	20	50
Cynipidae [6]	1900	150	40	10	2
Pompilidae	3200	200	40	15	1·25
Serphidae [7]	150	10	8	3	5·3
Scelionidae [9]	2000	230	100	25	5·0
Calliceratidae [7]	4400	25	50	7	12·5
Diapriidae [8]	1400	160	80	25	7·0
Belytidae [8]			20	7	

In the following groups the numbers of flightless species, where given, have been calculated by indirect means and are only very approximate.

Tiphiidae plus Scoliidae [10]	1000	20	20	—	2·0
Torymidae	—	—	—	—	15·0
Pteromalidae	—	—	—	—	0·75
Eupelmidae	—	—	—	—	12·0
Encyrtidae	—	—	—	—	4·0
Eulophidae	—	—	—	—	0·2
Chalcidoidea [10]	7000	700	300	—	4·0
Ichneumonidae [10]	13000	1000	250	—	2·0
Braconidae [10]	5000	430	—	—	0·1

[1] Mickel (1928). [2] André (1903). [3] Turner (1910). [4] Grandi (1928).
[5] Kieffer (1914). [6] Kieffer (1910). [7] Kieffer (1914a). [8] Kieffer (1916).
[9] Kieffer (1926). [10] Handlirsch (1925).

Summarising the data contained in these tables: there are about 12 groups in which all the species have wingless forms; these groups contain about 8000 species distributed amongst about 380 genera. There are about 20 groups containing a proportion of flightless forms, and these contain a total of about 37,000 species of which about 1300 are flightless. Handlirsch (1925) gives the figure of 70,000 for the total number of species in the Hymenoptera; of this total therefore about 45,000 belong to groups containing flightless forms and the remaining 25,000 to groups in which there are no flightless forms. The major groups containing no flightless forms are as follows :—Phytophaga 4000 spp., Terebrantian groups (EVANIIDAE etc.) 1000, VESPIDAE 3000, Sphecoids and Bees 17,000. The total number of flightless species is in the neighbourhood of 9300, which is about 13% of the total number of species in the Hymenoptera (70,000).

VIII. *Discussion and summary.*

Types of modification.

From the foregoing descriptions of the wingless thorax among the various groups of Hymenoptera, it is possible to pick out certain fairly well-marked types. The recognition of these distinct types is to some extent an arbitrary process, but speaking generally all the wingless forms in any group correspond to one of these types.

In assigning a group to one of these main types, the group is placed mainly on the thoracic structure of the more highly modified wingless forms, as the less modified ones are usually in the early stages of change towards the type displayed by the former. Since most of the important modifications occur in the dorsum of the thorax, the types of modification recognised are based upon characters of the dorsum.

In type I the dorsum is fused into one continuous surface. Occasionally faint traces of sutures are visible but the various parts of the dorsum form a continuous convex surface and are not distinguished from one another by any marked differences of contour. This type combines a very high degree of modification with the maximum degree of simplification. The MUTILLIDAE and some of the ants belong to this type; the latter belong principally to the CERAPACHYINAE and certain of the tribes of the PONERINAE such as the Proceratiini and Cylindromyrmicini.

In type II the dorsum is sharply divided into two parts. This type can be subdivided into two subtypes; in the first of these (a) the division of the dorsum is between the pronotum and the fused remainder; in the second (b) the division is between the propodeum and the remainder. The best examples of (a) are the MYRMOSIDAE, APTEROGYNIDAE, etc., but certain of the AGAONIDAE also belong here and some of the ants; e.g. *Dorylus*, and the Scelionid *Parabaeus ruficornis*. Subtype (b) contains the Ichneumonids and Braconids typified by the females of *Gelis*. Certain of the ants may be placed here also; e.g. *Eciton pilosum* and *E. crassicorne* (DORYLINAE), and certain MYRMICINAE of the tribe Cryptocerini.

In type III the dorsum may be considered to be divided into three major parts: the pronotum, the mesonotum, and the propodeum; the metanotum is usually fused with the mesonotum or propodeum or forms a deep groove between the two. This type may also be divided into two subtypes :—(a) in which the pronotum is enlarged and usually extended posteriorly, and (b) in which the pronotum is not altered. (a) may be further subdivided into two classes: (i) contains those forms in which the mesoscutum becomes much

reduced; (ii) contains the remainder in which there is no alteration in the relative sizes of the two, or in which the scutellum is reduced.

(i) contains the TIPHIIDAE, THYNNIDAE, SCLEROGIBBIDAE and most of the BETHYLIDAE typified by such forms as *Pristocera* and *Scleroderma*.

(ii) includes the EMBOLEMIDAE, POMPILIDAE, a few BETHYLIDAE such as *Mesitius*, the DRYINIDAE, some AGAONIDAE and TORYMIDAE, certain PROCTOTRUPIDAE (CALLICERATIDAE) and many sections of the ants.

Subtype (b) contains many of the forms that are only slightly modified, as for example the CYNIPIDAE and the Chalcidids other than the AGAONIDAE and TORYMIDAE. The PROCTOTRUPIDAE, DIAPRIIDAE, and SCELIONIDAE belong here and also many ants.

The wide range of thoracic modification that occurs among worker ants is shown by the fact that the FORMICIDAE are distributed among all the types.

Correlation between degree of modification and degree of wing reduction.

As might be expected, the degree of modification of the thorax depends to some extent upon the degree of reduction of the wings. It is true to say that where the wings show only a moderate degree of shortening and reach at least to the back of the propodeum, the modifications of the thorax, with few exceptions, are slight and do not go beyond a reduction in size of the mesothorax. An exception is *Olixon testaceum* Cam., and other Pompilids of the genus *Psyllosphex*; the fore-wings of *Olixon* reach beyond the back of the propodeum, yet the thorax is considerably modified (Reid, 1939 : fig. 1a). At the other extreme it is true to say that where the thorax is very highly modified, *e.g.* MUTILLIDAE and MYRMOSIDAE, the wings and tegulae are always completely absent. In between these extremes of very slight and very great thoracic modification, there is no close correlation of the amount of modification with the amount of reduction of the wings. For example, many Proctotrupids, e.g. *Calliceras* and *Conostigmus* spp., and many Cynipids have the tegulae reduced in size and the fore-wings reduced to stumps scarcely larger than the tegulae and yet the thoraces show extremely little modification. Other forms with the wings and tegulae no more reduced (species of *Promesitius*, fig. 45; *Braunsomeria*, figs. 38, 39; *Psyllosphex*, figs. 55, 56) show a high degree of thoracic modification.

Order in which the parts of the thorax are modified.

The modification of the various parts of the thorax, other than the wings, appears often to follow a definite order much the same for all groups, but modified in different ways in different groups. Probably the muscles of flight are the first structures to be reduced, followed by the pre- and postphragmata. The latter appear to be the first sclerotised structures to show change, for Salt (1937) has shown that the flightless males of *Trichogramma semblidis* lack the enormous postphragma present in the fully winged males, and yet the thorax of the flightless males is only slightly modified externally (see p. 434). The same thing occurs in the wingless males of *Cephalonomia quadridentata* Duch. (Van Emden, 1931; see also pages 403 and 404 of this paper) and in ants (see also figures of Janet (1907) and Lubbock (1879)). As has been stated on page 374, the first external part of the thorax to show change is the mesonotum; when this has undergone considerable reduction in size other parts of the thorax may commence to show radical change. The metanotum and the pleura are probably the next and by the time that the mesonotum has undergone considerable simplification there has probably been some loss of sutures on the

pleura. The last areas of the thorax to show considerable reduction are the meso- and metasterna. The prepectus may be unchanged unless the forelegs become more powerful; *e.g.* SCLEROGIBBIDAE.

Possible causes of flightlessness.

The discussion of which part of the thorax is the first to show change on loss of the power of flight leads one to speculate on what may be the original causes of flightlessness. The immediate structural causes are obvious enough, though even here it is not possible to say which cause is the first to operate; for example, do the wings shorten before the muscles atrophy or *vice versa*? The simplest generalised answer is that the modifications are adaptations to particular habits, which implies that the habits have determined the structure, *i.e.* they changed first, and not the reverse. For example, so far as their habits are known the SCOLIIDAE and TIPHIIDAE are all parasites of beetle larvae and the females burrow in the ground in search of their prey, but only a small percentage of the species are flightless (2%) so that there can be very little doubt that the habits of the families were established long before these few species lost their wings.

If it is true that reduction of the wings is usually an adaptation to special habits, and this certainly appears to be true of ectoparasitic insects of whatever order, then in most groups of the Hymenoptera the particular habit seems to be that of living or hunting in the ground; for example, the ants, Tiphiids and many Bethylids. Although it is true that most Tiphiids and Bethylids retain their wings, all worker ants are wingless and they are held to be, among Hymenoptera, the best adapted to living in the ground and similar situations. The male AGAONIDAE spend their lives inside figs, a situation which so far as the factors of space, light and humidity are concerned is not very dissimilar to the soil. I am not aware that the females of *Gelis* and other wingless Ichneumonids are particularly terricolous in habits; they mostly parasitise the cocoons of other insects upon plants. The reduction of the eyes and ocelli that occurs in many wingless forms may be in some instances an adaptation to hypogeichabits, and the same may be true of the testaceous or ferruginous colour characteristic of some wingless forms; at any rate it is a fact that among the ants the more strictly hypogeic forms are the most often pale in colour.

Correlation between modification of the thorax and modification of other structures.

There is some evidence that certain features that apparently have no direct connection with flight tend to be abnormal in flightless forms. Many wingless insects show reduction in the size of the eyes and ocelli; for example, worker ants normally lack ocelli, and certain species have even entirely lost the eyes as well (many DORYLINAE and others). The females of the MUTILLIDAE, APTEROGYNIDAE, BRADYNOBOENIDAE, etc., lack ocelli and the females of many species of *Pristocera* have eyes that are very much reduced in size. There are exceptions to this general rule; *e.g.* the females of *Gonatopus* and allied genera where the eyes are large and prominent, but these large eyes are probably adapted to the raptorial habits of the insect.

Since in the majority of flightless species it is only one sex that is flightless, such effects as the reduction in size of the eyes and ocelli might possibly be due to simple sexual dimorphism, independent of the reduction of the wings. But since in species where both sexes are fully winged neither normally shows any

marked reduction in the size of the eyes or ocelli (though those of the male may be abnormally large), this explanation is not a likely one. Furthermore it can be shown in a few instances that this reduction takes place in species which have both winged and wingless forms of one sex. Strickland (1912) records that the ocelli of the wingless males of *Gelis* (= *Pezomachus*) *flavocinctus* (Ashm.) are smaller than those of the winged males. Then there is the whole family FORMICIDAE in which the functional females possess ocelli while the workers lack them. Thus there seems to be a strong probability that reduction of the eyes and ocelli is correlated in some way, perhaps by the habits, with reduction in the powers of flight.

I have noticed two other characters which possibly have a tendency to be modified in flightless forms. In some groups there is a distinct tendency for the wingless forms to have less sculpturing on the thorax than the winged forms. In the MUTILLIDAE the pleura of the females are usually smooth and only slightly punctured, while those of the males are rugosely punctured. Much the same applies to the MYRMOSIDAE and BRADYNOBOENIDAE, and to a lesser extent it is true of the THYNNIDAE, including *Methoca*. Though the female of *Methoca* lacks the rugose puncturing of the male, there is a tendency for the thorax to develop a striate sculpturing which may possibly be secondarily acquired after loss of the puncturing, if indeed such loss has occurred. In such genera as *Thynnus* the male may be almost without sculpturing and therefore no more rugose than the female. In the species of *Gelis* this loss of sculpturing is best seen on the propodeum where there is a characteristic pattern of ridges; compared with those of the males the propodeal ridges of the females are considerably reduced. However, against these examples must be set a great many exceptions.

The other character is the colour of the cuticle, particularly on the thorax. There appears to be a slight tendency for the development of a ferruginous or testaceous colour in wingless forms where the winged forms of the same species are black. For example, the thorax of the males of *Myrmosa* is black, that of the females ferruginous; the same is true of *Bradynoboenus gayi*, *Methoca ichneumonides*, and some of the other species of *Methoca*, but not all. The male and female of *Mutilla europaea* form a good example, but there is a very large number of exceptions in the MUTILLIDAE. The prevailing colour of the females of the MERIINAE is black and ferruginous red and there is perhaps more red among the females of *Pseudomeria* and *Braunsomeria*, in which genera wing reduction is common. Many of the wingless females in the Bethylid genera *Pristocera*, *Scleroderma*, *Apenesia*, *Cephalonomia*, etc., are ferruginous. The females of the EMBOLEMIDAE and SCLEROGIBBIDAE are ferruginous, the males darker to black. The males of the AGAONIDAE are ferruginous, the females usually black. The thorax of the females of *Gelis* (and much of the abdomen also) is frequently ferruginous while that of the males is usually black. There are a great many exceptions to this tendency and I have not noticed that in those species where winged and wingless forms of one sex occur, the wingless form is more ferruginous than the winged.

Another feature common to many wingless Hymenoptera which has already been referred to, is an increase in the size of the legs; this is well seen in most wingless Scolioids and Bethylids and is also shown by the SCLEROGIBBIDAE, AGAONIDAE and some ants. The wingless males of *Trichogramma semblidis* (Salt, 1937) have stouter legs than the winged males. A marked increase in the size of the legs is usually accompanied by an increase in size of some parts of the thorax, presumably to accommodate the larger coxal muscles; this is very

obvious in the female Scleroglbbidae (fig. 53) where the forelegs, particularly the femora, are extremely powerful and the pronotum is of great size, serving as a roof to the correspondingly large prepectus to which the coxal muscles are attached.

One may suggest that the reduction in size of the wings, eyes, and ocelli, and the increase in size of the legs, are all adaptations to particular modes of life such as that of burrowing (see p. 440); but if the reduction of thoracic sculpturing is a genuine effect really correlated with loss of the wings, it seems difficult to explain.

Degrees of difference to be expected between winged and wingless forms of one sex of one species.

The discussion of the differences that may exist between the winged and wingless forms of one sex of a species, leads me to consider this question from the point of view of the systematist, to whom it is of interest to know what order of difference may be expected within the limits of a species. The only generalisation that one can make is that if two forms differ only in the length of the wings and the shape of the thorax, then it is unlikely that they belong to different species; if they do differ in other characters they may belong to different species, but not necessarily so. The ants provide the most extreme examples of differences between winged and wingless forms of one sex of a species. If one neglects the ants in which the workers form a highly specialised cast, and perhaps also the Cynipids where the winged and wingless females form alternating generations, then one can form some idea of the maximum amount of difference that is likely to exist between the winged and wingless forms of one sex of any one species. It has been shown that reduction of the wings always leads to reduction in the size of the thorax, particularly the mesonotum. Reduction in the size of the mesonotum often leads to some obliteration of its division such as the notaulices and parapsidal furrows. This simplification of the mesonotum may proceed far enough (*e.g.*, wingless males of *Cephalonomia quadridentata*) to cause fusion of the scutum and scutellum. Reduction in size of the mesonotum usually causes some change of shape in the pronotum. In short, differences in the thorax of flightless forms are to be expected and may amount to a considerable reduction in size with simplification of the mesonotum and a small degree of fusion between parts. In addition the eyes and ocelli of the wingless forms may be somewhat smaller (Strickland, 1912), and it is possible that the sculpturing of the thorax may show some reduction and the legs may be more powerful. Beyond these points no sharp differences are likely, and if such exist the inference is that the forms which display them belong to different species. The case of *Trichogramma semblidis*, already referred to (p. 434), is an awkward exception, for though the stouter legs of the flightless males may be correlated with the reduction of the wings, there are also important differences in the antennae that would normally be considered of at least specific value.

Summary.

This survey of the wingless Hymenoptera shows that in groups where forms with much-modified thoraces occur, the structure of such thoraces sometimes gives strong indications of affinities. It is among the groups that comprise Ashmead's Vespoidea that most of the highly modified forms occur, and it is in these groups that the wingless thorax has thrown most light on affinities.

Where these groups are concerned a study of the wingless thorax, supplemented by examination of other characters, gives valuable clues to the interrelationships of the families (see pp. 396 and 416). Outside this group of families the wingless thorax has not yielded much new data, largely because the wingless forms are scarcer and not often highly modified.

In the FORMICIDAE the characters of the worker thorax are on the whole in agreement with the accepted classification of the ants; only very seldom do they seem to be contradictory, *e.g.*, *Melissotarsus*.

The Proctotrupoidea contain a few very modified wingless forms each of which tends to display the thoracic characters of its family in an exaggerated form.

The CYNIPIDAE show only slight modification.

In the Chalcidoidea, with the exception of the males of the AGAONIDAE and of some TORYMIDAE, modification is slight and usually leads to exaggeration of the thoracic " facies " of the family to which the flightless form belongs, *e.g.*, EUPELMIDAE. The thorax of the flightless males of the AGAONIDAE and TORYMIDAE is highly modified, displays a wide range of structure, and is sometimes very difficult to interpret.

Among the ICHNEUMONIDAE and BRACONIDAE there are only a few genera of Cryptine Ichneumonids (*Gelis* (= *Pezomachus*) in particular) which contain wingless forms with highly modified thoraces. The appearance and structure of the thorax in these forms is rather unlike any other except perhaps some ants; but the ants usually show some enlargement of the pronotum and this is not found in *Gelis*.

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Note :—All the figures have been drawn using a binocular microscope and squared eyepiece.

In figures of winged thoraces the cross-hatched areas indicate the areas of insertion of the wings. These areas have not been accurately drawn as they are complex and have not been considered in the present paper.

Explanation of Symbols.

These are for the most part the same as those used by Snodgrass (1910). The figures 1, 2, 3, placed after and below a symbol indicate that the area designated by the symbol belongs to the pro-, meso-, or metathorax respectively, except in the instances of the second and third spiracles, Sp_2 and Sp_3. The former, largely as a matter of convenience and in order to meet the practice of myrmecologists, is referred to in the text as the " metathoracic " spiracle; the latter (Sp_3) is the propodeal spiracle. The Roman numerals I, II, III, etc., placed before a symbol or standing alone, indicate 1st, 2nd, or 3rd abdominal segment, etc.

A, postero-lateral suture of the prepectus.
a, anterior edge of mesoscutum seen through pronotum.
ax, axillary region or notal axilla.
Axl, axillary ridge.
B, meso-metapleural suture.
C, metapleural-propodeal suture.
Cx, coxa.
E, metanotal-propodeal suture.
Edp, endophragmal pit.
Eps, epimeron.
Fp, furcal pit.
IT, propodeum.
k, transcutal suture.
N, notum.
No, notaulix.
Pa, parapsis.
Pf, parapsidal furrow.
Pl, pleuron.
PN, postnotum.
Ppct, prepectus.
Ps, pleural suture (separates episternum from epimeron).
Psc, prescutum.
Ptg, post-tegula.
q, sterno-pleural suture.
R, parascutal ridge.
r, horizontal suture dividing pleuron into dorsal and ventral portions.
S, sternum.
Scl, scutellum.
Sct, scutum.
Sp, spiracle.
Ss, scutellar or metanotal scale.
T, tarsal segment.
Tb, tibia.
Tg, tegula.
Vnr, scuto-scutellar suture.
W, wing.
Wp, wing process.